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Changes in Responsiveness to a Constant Stimulus

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1. Introduction

A constant stimulus presented at intervals to an animal does not evoke a constant response: it is therefore necessary to postulate changes in the animal's internal state. The nature of these changes presents one of the central problems in animal behaviour studies. In recent years the theories of Lorenz and Tinbergen have greatly facilitated progress in this field: the main purpose of the present paper is to consider these theories in the light of some recent observations and experiments.

2. The Basis of Changes in Responsiveness

The changes in the internal state of an animal which are responsible for its changes in responsiveness to a constant stimulus could be of two types:

(*a*) Changes in factors external to the CNS which act on the nervous system—e.g. hormones, "hunger pangs" from the stomach, and so on.

(*b*) Changes in one or more parts of the nervous mechanism mediating the response, which changes are *temporarily* independent of factors external to the central nervous system.

The available evidence is clearly in favour of the latter view, thus:

(i) It is not possible to ascribe all motivation to extra-neural irritants—hunger to hunger pangs, male sexual behaviour to distended seminal vesicles, and so on (see Morgan, 1943; Hebb, 1949). Changes in motivation are often independent of the arousal or satisfaction of any need. Thus van Iersel (1953) has shown that the mere performance of courtship behaviour causes a drop in the sex drive of the Three-spined Stickleback, though the decrease is not so great as that caused by the consummatory act of fertilisation. Similarly Tinbergen and Perdeck (1951) record that the intensity of the begging response of young Herring Gull (*Larus argentatus*) chicks falls off with successive presentations of the dummy: they distinguish this from the longer lasting habituation. Lorenz (1935, 1937) and a number of other authors have given instances of the occurrence of hunting or food-seeking behaviour apparently independently of any need for food—e.g. the sucking of human infants and other mammals (Ribble, 1943, quoted by Hilgard, 1948; see also Davis et al., 1948, quoted by Stevens, 1951; Ross, 1951, and refs. cited), the gnawing of rats (Keeler, 1946), the hunting of a young satiated owl (Thorpe, 1948), the "paper tearing" of tits (Logan Home, 1953; Hinde, 1953a); additional cases are cited by Tinbergen (1951). Janowitz, Hanson and Grossman (1949) have shown that the daily intravenous administration of glucose has no significant effect on the food intake of the dog over periods of 2 to 9 days.

(ii) Experiments by Bellows (1939) and others (cited by Morgan & Stellar, 1950) on dogs with oesophageal fistulae indicate that drinking is not controlled directly by the water in the system. Even if the water which the dog drinks is allowed to drop out of the fistula, and so does not enter the stomach, it stops drinking after a while. "It is as if so much water deficit leads to so much drinking behaviour whether or not a bodily need is satisfied." These experiments support the view that drinking behaviour is controlled by a central nervous mechanism whose state is controlled by extra-neural factors, though this extra-neural control takes some time to act. More detailed experiments leading to the same conclusion are cited on pages 42 and 48-49.

(iii) This suggestion is also supported by the work of Stellar & Hill (1952) on drinking in rats. These workers found that when a rat drinks it does so at a constant rate—6 to 7 tongue laps or 0.03 c.c. of water per second. When thirsty rats are given water they drink steadily at this rate for a few minutes, and then drink in short bursts over the ensuing period. For periods of deprivation of between 48 and 168 hours the initial period of continuous drinking is virtually constant (c.8 minutes), though subsequently the animals which have been deprived longer drink more frequently. "The important variable is the frequency of alterations between resting and drinking. As the amount of deprivation increases, the length

of the rests decreases and the frequency at which bursts of drinking occur increases." These results can be interpreted in terms of a central mechanism which is in immediate control of the drinking behaviour, whose state is influenced, though with some delay, by extra-neural factors, and which is fully activated after a deprivation of about 48 hours. (Stellar & Hill state that the interruptions in drinking represent some positive interference rather than mere temporary satiation because, when the rats stop drinking, they do something else. But it is of course equally legitimate to argue that these other activities are permitted to appear because the tendency to drink is temporarily low.)

(iv) A number of other studies suggest that at least one of the roles of the extra-neural factors is to influence changes in a nervous mechanism. Thus Beach and Holz-Tucker (1949) have shown that, in castrated male rats, the frequency of intromissions increases and the refractory period after ejaculation decreases with successively larger doses of male sex hormone.

(v) Further indirect evidence is afforded by studies showing that the performance of an activity itself may serve as a reinforcement, even though there is no change in "need." Thus Sheffield & Roby (1950) have shown that a non-nourishing but sweet tasting substance can be an effective reward for instrumental learning, and suggest that the "elicitation of the consummatory response appears to be a more critical *primary* reinforcing factor in instrumental learning than the drive reduction subsequently achieved." This of course imposes a limit on need reduction theories of learning such as those of Hull. Similarly Sheffield, Wulff & Backer (1951) have shown that copulation without ejaculation, and thus apparently without need reduction, can also act as a reinforcement for sexually naive male rats. Harlow et al. (1950) have shown that the mere manipulation of a puzzle is sufficient to produce learning in monkeys, even though no food is given. Grindley's (1929) finding that young chicks would show some temporary increase in running speed to food, even though they were only permitted to see the food through glass, suggests that the perception of the reward was important; and Wolfe & Kaplon (1941), also working with chicks, found that the amount of consummatory behaviour was more important than the reward. Wolpe (1950) has cited additional cases.

These experiments do not, of course, distinguish adequately between the effects of the performance of the consummatory act and the effects of the perception of the relevant stimuli. Kohn (1951) and Berkun, Miller & Kessen (1952) have shown that (i) milk administered by mouth reduces the hunger of rats (as measured either by a consummatory or an instrumental response) more than milk introduced directly into the stomach, and (ii) milk introduced directly into the stomach reduces hunger more than saline similarly introduced. The effects of mouth feeding could be due to the sight, smell or taste of food as well as to the act of swallowing: the superiority of stomach milk over stomach saline must be due to interoceptive factors. Miller & Kessen (1952) have shown that milk introduced directly into the stomach can serve as a reward, though milk taken by mouth is more effective: they point out that the faster learning of the animals which received milk by mouth might be expected from the fact that this procedure produces a greater reduction in the strength of the drive. (Hull, 1943, has suggested that the mastication of food brings about learning through secondary rather than primary reinforcement, but Miller & Kessen believe that this can be reduced to the same factor of "drive reduction".)

For present purposes, however, the relative effectiveness of the proprioceptive stimuli which result from the performance of the activity, and of the other stimuli which the animal encounters, is not particularly relevant. The important point in Sheffield's experiments is that learning **may** occur without reduction in *need*: reduction in "drive," which is defined by Thorpe (1951a) as "The complex of internal states and stimuli leading to a given behaviour," and thus includes the state of the nervous mechanism, may be involved.*

These considerations suggest, then, that the tendency for any particular activity to appear depends on the state of the nervous mechanism underlying it. The performance of the behaviour causes (either directly or indirectly) changes in this state. Thus a change in the tendency for the activity to appear involves changes in the state of the nervous mechanism, but not *necessarily* in the extra-neural factors which

* The term "drive" has been used sometimes to refer to the state of the mechanism, sometimes to the factors which influence that state, and sometimes to both (Hinde, 1953b).

contribute to that state—though of course changes in these factors may occur.

This view that changes in responsiveness are due in the first instance to changes in the state of a nervous mechanism rather than the reduction of a need is contrary to Hull's (1943) attitude, but in line with the suggestions of a number of other workers. Thus Beach (1942a) suggested that "sexual arousal depends upon the creation and maintenance within the central nervous system of a condition analogous to Sherrington's *central excitatory state*", and quotes evidence that "sexual excitability may depend in part upon the function of tissue which apparently contributes nothing to the organisation of the motor elements of mating." Similarly Pavlov (1928) postulated a food centre whose activity could be modified by both internal and external stimuli, and Morgan (1943) suggested a "central motive state" to account for the facts of feeding, drinking, sexual and other forms of behaviour. These authors recognise that the central state may be influenced by hormonal agents or by the internal stimuli.

3. The Analogies used by Lorenz and Tinbergen

Lorenz (e.g. 1950) has provided a model for such changes in the state of the central nervous mechanisms with his "reservoir" of "reaction specific energy"—the performance of each type of instinctive behaviour is supposed to be associated with the discharge of "reaction specific energy" from a reservoir specific to the response. The intensity of the response (i.e. the rate of outflow) is supposed to depend in part on the level in the reservoir, and in part on the extent to which a spring-valve has been opened by the stimulus.

This analogy has been (and still is—see Precht, 1952) of immense value in stimulating research and co-ordinating its results, but it suffers from a number of disadvantages. To provide an adequate model for the detailed course of an instinctive response, a very complicated hydraulic system must be postulated; and the relations between the components of this system and those of the actual mechanism underlying the behaviour are, to say the least, extremely vague. Further, doubt has been cast on the degree of specificity of the "reaction specific energy" by the occurrence of displacement activities and other phenomena.

Lorenz was concerned primarily with the properties of individual responses. In his recent book Tinbergen (1951) has elaborated a scheme which takes account also of the many different types of behaviour shown by an animal. He does not mention the concept of "reaction specific energy" (although he does stress the specficity of causal factors), but refers instead to "nervous centres" "loaded" with "motivational impulses" which are subsequently discharged. This has the advantage of avoiding the comparison with the details of a hydraulic system, but it retains the idea of something stored and then flowing away in the course of the response. Further, the concept of motivational impulses, which was intended by Tinbergen only as a provisional analogy, cannot easily be related to measurable aspects of behaviour.

At a conference in Cambridge in 1949 the term Specific Action Potential (SAP) was proposed (with the approval of both Lorenz and Tinbergen) to describe the potentiality of an animal for showing a particular type of behaviour. Thorpe (1951a) has defined Specific Action Potential (which could perhaps better be called Specific Action Potentiality) as follows:

"The state of the animal responsible for its readiness to perform the behaviour patterns of one instinct in preference to all other behaviour patterns. This specific readiness diminishes or disappears when the consummatory act of the charged instinct has been performed."

Two points about this definition must be made. First, SAP is defined as a state of the animal: eventually a definition in terms of experimentally observable quantities (such as intensity of response to a given stimulus, but see p. 51) will be necessary. Second, it is not clear from the definition whether SAP refers to the readiness to perform one particular activity (e.g. ejaculation) or a group of related ones (e.g. courtship, mounting, intromission, ejaculation). It is likely that the term would be more valuable in practice if it referred—as its name implies—to one activity only. Of course since functionally related activities often share causal factors (p. 44), relations between the SAPs of related activities are to be expected.

With these reservations, the term SAP has two advantages over its predecessors:

(i) It is, at least theoretically, open to quantitative treatment (but see p. 51)

(ii) It is essentially a molar concept. Its

measurement depends on the direct observation of behaviour, and does not involve any unnecessary assumptions about the nature of the underlying nervous mechanisms. Such assumptions are, of course, necessarily involved in a theory postulating a flow of "motivational impulses." This is not to imply, of course, that the study of behaviour should not be related to neurophysiology—the case for relating behavioural and neurophysiological data as put by Hebb (1951) is unanswerable. But it is unwise to assign a *central* position in a theory of behaviour to quasi-neurophysiological concepts like "motivational impulses," whose status is not experimentally verifiable. Their use may lead to blind alleys of theory.

In the following sections the applications of the concept of SAP to certain aspects of behaviour study—and in particular to Tinbergen's theory of the hierarchical organisation of behaviour—are considered. It must be emphasised from the start that, although the main purpose of this paper is to suggest that analogies of anything flowing (other than the nervous impulse, of course) may sometimes be misleading, in nearly every other respect Tinbergen's theory of the hierarchical organisation of behaviour is followed closely. The extent to which the discussion depends on Tinbergen's work will be abundantly clear throughout.

4. The Heirarchical Organisation of Behaviour

Before considering further the concept of SAP, it is necessary to review very briefly the evidence for the hierarchical organisation of behaviour as presented by Tinbergen (1942, 1951) for the Three-spined Stickleback (*Gasterosteus aculeatus*), Baerends (1941) for the Digger Wasp (*Ammophila campestris*), Baerends & Baerends-van Roon (1950) for various Cichlid fishes, and also by Räber (1948) for the Turkey (*Meleagris sp.*) and Hinde (1953c) for the Great Tit (*Parus major*). The argument can be divided into four stages; reference may be made to the papers cited above for further details:—

(i) Evidence for a hierarchical system of causal factors. It is found that some causal factors influence a number of different activities, whereas others influence a few or only one. The causal factors which influence a group of activities can thus be classified in a hierarchical scheme. At this stage in the argument such a scheme could be no more than a convenient method of classifying the data.

Thus, injections of testosterone propionate influence the appearance of singing, courtship, reproductive fighting, etc., in the Chaffinch (*Fringilla coelebs*), and each of these groups of activities are influenced by other causal factors which are specific to them (Hinde, unpublished experiments). Further, within each of these groups of activities, particular patterns of behaviour are influenced by further factors which have an even greater specificity.

(ii) Evidence for a hierarchical system of behaviour. Observation shows that for each complex of causal factors, the animal shows a particular type of appetitive behaviour or consummatory act. These types of behaviour can thus also be arranged in a hierarchical manner.

Thus, when certain causal factors are present, a Chaffinch shows a particular type of appetitive behaviour which we call migration. If other complexes of causal factors are present, it will show other types of appetitive behaviour—"looking for" a mate, "looking for" a nest site, "looking for" nest material and so on. Each type of behaviour can be characterised by (*a*) the motor pattern, (*b*) the orientation component, and (*c*) the sets of stimuli to which the animal is particularly responsive while showing the behaviour.

(iii) The hierarchical system of nervous mechanisms. It may be accepted as axiomatic that behaviour is mediated by the nervous system, and that every particular pattern of behaviour is mediated by a particular nervous mechanism or pattern of nervous activity. Since the types of behaviour shown by an animal can be arranged in hierarchical systems, there must be hierarchical systems of nervous mechanisms which correspond to them. The nervous mechanisms involved need not, of course, be anatomically localised, nor need the functional levels in the hierarchy necessarily correspond to anatomical levels in the nervous system.

(iv) Evidence for causal relations between the different levels in the hierarchy. Even if the nervous mechanisms can be considered to be arranged in a hierarchical manner, additional evidence is necessary before causal relations between the different parts of the hierarchy can be established. It would be possible for the causal factors at, say, the top

level in one of the hierarchical systems to act simultaneously but *independently* on the subordinated mechanisms: the uneconomical and improbable sound of such an arrangement could arise from a naiveté in our ideas about the functioning of the nervous system. In fact the evidence for causal relations between the different levels, though considerable, is still far from conclusive. Much of it has been given in the studies cited above (esp. Tinbergen, 1951), but three points may be mentioned here:

(*a*) There are a number of cases in which several different but functionally related activities have been evoked by stimulation of a limited area of the brain. These have been cited elsewhere (Tinbergen, 1951; Hinde, 1953c).

(*b*) Tinbergen suggests that hormones act only or mainly on the higher centres in the reproductive instinct of the Stickleback. If this is the case, it provides important evidence for functional connections between the levels of the hierarchy, for activities of the level of the consummatory act are, of course, affected by the appropriate hormones. Evidence on this point from studies of other animals on the whole supports Tinbergen's view, but it is certainly not conclusive. Thus Collias (1950) quotes Kent (1948) as finding that progesterone had a more rapid effect on spayed guinea pigs (previously treated with oestrogen) when it was injected directly into the brain vesicles than when administered more peripherally. Brookhart, Dey & Ranson (1941) found that restricted hypothalamic lesions eliminated the normal response of guinea pigs to sex hormones. Bard (1940), also working with mammals, believes that sex hormones exert their effects primarily on the hypothalamus. On the other hand, Beach (1947), in a review of the evidence (e.g. Maes, 1939), believes that "until there is convincing evidence to indicate the limit of hormonal action, it would appear safest to assume that gonadal hormones affect all of the nervous units involved in mating activity."

(*c*) The various types of reproductive activity of the Great Tit (Hinde, 1952, 1953c) show similar diurnal rhythms in frequency of occurrence. Similar data are available for many other species (see, e.g., Palmgren, 1949). Further, in the Great Tit and in many finches (*Fringillidae*) different types of reproductive behaviour often occur together in outbursts which are interspersed with periods of non-reproductive behaviour. Such facts as these could be due to independent but more or less simultaneous changes in the causal factors or mechanisms which control the various activities, but it is at least a plausible hypothesis that they are due to changes in a superordinated mechanism.

This division of the argument relating to hierarchical systems* into four stages facilitates its evaluation. In the opinion of the writer the evidence for a hierarchical organisation of *behaviour* is well established in outline by the studies of the Stickleback, Digger Wasp, Cichlid fishes, Turkey and Great Tit cited above—though the details are far from clear and there is particular need for more detailed descriptions of the types of appetitive behaviour shown by animals in nature. This hierarchical system of behaviour provides a starting point for the study of the whole behaviour of a species, and makes it possible for such a study to be integrative as well as analytical. The evidence for a hierarchical system of causally related nervous mechanisms is as yet sketchy, but sufficient to justify its acceptance as a working hypothesis.

As we have seen already, however, Tinbergen considers his nervous mechanisms as being "loaded" with "motivational impulses" from various sources—the "flowing away" of motivational impulses from each centre of the level of the consummatory act being associated with muscular movements mediated by that centre and a decreased tendency to respond again. This analogy of flowing "motivational impulses," however, quickly leads to a series of other assumptions and postulates, of which the following may be mentioned:

(i) The functional relations of the system are one-way—i.e. the higher levels can affect the lower ones but not vice versa.

(ii) A lowering of responsiveness (represented by the discharge of motivational impulses) is always associated with an activity of some sort—usually the performance of the consummatory act.

(iii) Each centre is prevented from discharging impulses continuously by the presence of a block, pictured as being just beneath it. This

* The suggested organisation of the nervous mechanisms into functional (but not necessarily anatomical) hierarchial systems corresponding to reproductive behaviour, feeding behaviour, etc., does not imply that the various systems are independent of each other. Many "low level" activities are shared by different systems, and causal relations exist between them.

block (which corresponds to the spring valve of the Lorenzian reservoir) is removed when the appropriate sign stimuli impinge on the "reflex-like innate releasing mechanism."

In the next section certain observations and experiments are considered in order to ascertain whether an analogy of "flowing" "motivational impulses," and these further ones which arise from it, are likely to have continued usefulness in the interpretation of behaviour. Since the aim is not to present a list of experimentally determined factors affecting any one particular response, the discussion is intentionally broad.

5. The Analogies used by Lorenz and Tinbergen Discussed in the Light of Some Recent Experiments

(*a*) The analogy of "flowing" "motivational impulses," and the assumption that the effects are one-way only.

(i) *General*

After the performance of an instinctive activity the threshold of stimulation necessary for its release is often temporarily raised. The effect may be specific to the response in question, to a group of functionally related responses, or only to the particular stimulus situation which released the response. The first case was pictured by Lorenz as a draining away of "reaction specific energy;" the second by Tinbergen as a draining away of "motivational impulses" from the appropriate sections of the hierarchical system. The third case (discussed further below) was regarded by Prechtl (1953) as due to an "adaptation in the afferent apparatus."

Of course, the models used by Lorenz and Tinbergen were not intended to imply that a reduction in the responsiveness of a nervous mechanism is necessarily accompanied by something flowing out of that mechanism, but they do tend to distract attention from the other possibilities which are open. Such a reduction in responsiveness could be due to a chemical or structural change resulting from the co-ordinated nervous discharge, to a change in the releasing mechanism, to a proprioceptive feed-back from the appropriate action-pattern, or to an inhibitory effect produced by stimuli resulting from the behaviour. The mechanism of the effect could be essentially similar in these latter cases. At present there is no way of deciding between the possibilities: all that can be said is that the performance of the response is associated with a *reduction in SAP.*

Sometimes groups of related activities may undergo parallel changes in SAP. Thus, eating often involves a reduction in the tendency to show the various hunting activities, as well as in the tendency to swallow. Such facts can be understood in terms of a hierarchical system without recourse to "draining away." Thus, the state of a particular nervous mechanism (say that underlying ejaculation) may, in common with a number of other nervous mechanisms (e.g. those underlying courtship) be influenced by a functionally superordinated mechanism (the "sexual centre"), whose own state may be influenced by the performance of the activity mediated by the lower centre (ejaculation)—perhaps through some sort of sensory feed-back.

Sometimes the performance of a response is associated with an *increase* in the tendency to perform the activity again—the phenomenon known as "warming up" or getting "worked up." It is impossible as yet to say whether the increased tendency is due to, or merely associated with, the performance of the activity. The effect can be described in terms of an increase in SAP, but only with difficulty in terms of motivational impulses.

(ii) *Displacement Activities*

Tinbergen (1940, 1952) has shown that when one pattern of behaviour, which is strongly motivated, is denied expression through the absence of the appropriate releasing stimuli, conflict with an incompatible pattern, or for any other reason, the animal may show an apparently irrelevant pattern of behaviour—a displacement activity. He has presented considerable evidence that the appearance of a particular pattern as a displacement activity may be influenced by the initial posture, the external stimuli present (whose importance had previously been stressed by Armstrong, 1950), the degree of "spontaneity" of the pattern, and possibly by which instincts are activated—in other words, by the previous state of the mechanism. Thus, the state of any particular mechanism may, under certain conditions which involve fairly intense thwarting of another pattern of behaviour, be influenced through the mechanisms which normally mediate that pattern.

This may be compared with experiments on behaviour motivated by an "irrelevant drive." Hull (1943) has suggested that patterns of behaviour may be influenced not only by the

drive strength appropriate to them, but also by drive strengths relevant to quite other patterns. This effect has been demonstrated in a number of cases (Webb, 1949; Siegel & Siegel, 1949; Amsel, 1950a; Amsel & Maltzman, 1950; Siegel & Brantley, 1951; Ullman, 1951, 1952). The processes involved are clearly complex, and it is necessary for the drives concerned to be of approximately the correct absolute and relative strengths: if the irrelevant drive produces a response incompatible with the one under investigation, it produces an interfering effect rather than a positive one (Kendler, 1945; Siegel, 1946; Amsel, 1950b; Estes & Skinner, 1941). In most of these cases the strong "relevant" drive was hunger or thirst, and the "irrelevant" one either the after effects of shock, or conditioned stimuli for shock. Beach (1947), however, quotes much evidence that "sexual mechanisms may be activated by non-sexual stimulation": some of his examples possess the characters of displacement activities, but many seem comparable with the cases cited above. The experimental design in many of these instances may have involved the thwarting of a tendency to flee, and, in so far as that was the case, the behaviour may be likened to displacement behaviour. It differs, however, from conventional displacement behaviour in that it is not irrelevant. The behaviour expected by the observer is shown, but at a higher intensity.

The precise mechanism by which the irrelevant drive augments the relevant one is in dispute. Hull's scheme implies that the interaction is largely independent of the momentary external stimulation and that it takes place by quantitative summation or subtraction. The experiments of Danziger (1953) throw doubt on this, and he has suggested an alternative explanation in terms of Pavlovian "mutual induction" between the centres concerned. It seems certain, however, that the facts cannot readily be accounted for in terms of "reaction specific energy" which is specific to a response: on a "motivational impulses" hypothesis the impulses are not to be considered as absolutely specific to a particular hierarchical system.

(*b*) A lowering of responsiveness is not necessarily due to the performance of an activity.

In Tinbergen's scheme a reduction in responsiveness is always associated with a change in the motor mechanism of the response—with the discharge of "motivational impulses" and the performance of motor behaviour. A number of recent studies have shown, however, that this is not necessarily the case.

In the first place, there may be inhibiting effects resulting from changes in the releasing mechanism. Thus Prechtl (1953), working with the gaping response of young Passerines, found that repeated evocation with one stimulus led to a waning of the response which was specific to the particular stimulus: the response could still be elicited by the use of other stimuli. He postulated, therefore, a process of adaptation in the innate releasing mechanism. This effect was a temporary one, and thus seems to be distinct from the sIR. (Hull, 1943) component in the extinction of conditioned responses which,although specific to the stimulus situation, is a permanent effect and similar to habituation. The temporary component in the extinction of conditioned responses (IR, Hull, *l.c.*) is not specific to the stimulus.

Few other data on this effect are available, but an experiment which is perhaps basically similar has been recorded by Grunt and Young (1952). If a male guinea pig copulates with a female with which he is confined, he shows little or no further interest in her during the hour following ejaculation. If, however, the female is replaced with a new one after thirty minutes, his sexual activity returns. If the first female is removed and then replaced, no comparable increase occurs. It thus seems that at least some of the lowered responsiveness shown by the male is specific to the particular female which first evoked his sexual behaviour.

Another line of work which may be relevant here is provided by studies of "spontaneous alternation" and related phenomena in rats. If rats are given a choice of two routes to a reward, both of which are of equal length, they show a marked tendency to alternate between the two on successive runs. Although a number of attempts have been made to explain this behaviour in terms of an inhibitory effect produced by each response (e.g. turning left) which reduces the tendency of the animal to show that response again, Glanzer (1953) has summarised convincing evidence that the behaviour should rather be interpreted mainly in terms of an alternation of the operative stimuli. He postulates "each moment an organism perceives a stimulus-object or stimulus objects, A, there develops a quantity of stimulus satiation to A . . . Stimulus satiation reduces the organism's tendency to make any response to A." The time

taken for the disappearance of the effect varies with the difference between the stimuli provided by the two pathways.*

The extent to which these rather diverse instances have a common causal basis must remain problematical, but they share the character that a reduction in the tendency to show a response seems to be related to the stimulus which evoked the response and not to the response itself. It is not easy to account for this in terms of a theory in which motivation depends on accumulated "motivational impulses" which can only be discharged in action.

In addition to the phenomenon of "satiation" to the stimuli which released a pattern of behaviour, it is also possible that an animal may show a change in behaviour as a result of stimuli other than those which evoked the behaviour—the stimuli which it was "looking for." This is recognised implicitly in Tinbergen's scheme: when the appetitive behaviour mediated by one centre brings the animal to a situation in which it is presented with the appropriate sign stimuli, the block below the centre is removed, the "motivational impulses" are allowed to flow to the subordinated centres, and the appetitive behaviour ceases. Thus, it has been suggested that the migration of some fishes (Tinbergen, 1951) and birds (Hinde, 1953c) comes to an end because the "habitat selection sign stimuli" release other types of behaviour associated with territory establishment. However, such an explanation involves the unproven assumption that the birds engage in reproductive behaviour (e.g. patrolling the territory) as soon as they stop migrating. An alternative explanation in terms of an inhibitory effect from the habitat selection releasing mechanism to the nervous mechanism mediating migration is at least possible. In subjective terms, the birds recognise a suitable habitat and so stop migrating.

A similar explanation could be applied to a number of other cases. A male Chaffinch paired with a female and kept in an aviary in early Spring, before courtship proper has begun, behaves very much as a winter bird. A male Chaffinch kept alone in similar circumstances sings a great deal and spends much time in flying to and fro—behaviour which should probably be regarded as appetitive behaviour "aimed" at finding a mate. It thus seems that the presence of the female "satisfies" the male, and the appetitive behaviour is inhibited. Similarly, wild male Great and Blue Tits, at the same time of year, will feed quietly while in company with the female, but if she flies off they will begin to sing and to search for her (Hinde, 1952). Here, of course, a simple inhibitory effect from the releasing mechanism is not sufficient to explain the behaviour—an intermittent glimpse of the female may be sufficient, so that there must be some process which "carries" the effects of these glimpses over the intervening periods. Other similar cases can be seen in the behaviour of the Cormorant (*Phalacrocorax carbo*. Koortlandt, personal communication).

More precise observations, pointing to the same conclusion, are available at the level of the consummatory act. Thus, Janowitz and Grossman (1949) have shown that the cessation of eating in dogs is governed by stimuli resulting from the eating behaviour itself. They divided the relevant factors into oral (i.e. all the effects on the head receptors involved in the act of ingestion) and gastric (those resulting from the presence of the food in the stomach). They found that, in oesophagostomized dogs, the amount of sham feeding before satiation greatly exceeded the food deficit—indicating that oral factors alone may produce cessation of eating, but that they are less effective than oral and gastric factors together. Normally, oral and gastric factors co-operate. Similarly, Lorber, Komarov & Shay (1950) found that sham feeding produced an almost immediate cessation of gastric motor activity; and Hill et al. (1952) found that various substances placed by fistula in the jejunum of a dog reduced the food intake about an hour later. The experiments of Kohn (1951) and Berkun, Miller & Kessen (1952), quoted on p. 42, also show that proprioceptive and/or interoceptive stimuli normally resulting from the performance of the consummatory act are important in drive reduction.

Conclusions somewhat similar to those of Janowitz & Grossman were reached by Towbin (1949) for drinking. He writes: "The satiation of thirst that immediately follows drinking is apparently brought about by the summation of afferent impulses that result from the drinking

* It may be noted that Glanzer's analysis does not demonstrate that there is *no* inhibitory effect produced by the response: if there is one, it may be considered as comparable to the other cases of an inhibitory effect produced by stimuli (in this case proprioceptive) resulting from the behaviour cited in the following paragraphs.

itself. However, this is a temporary satiation, for if no water actually enters the internal environment (esophagostomy) the dog will, within a few minutes, again exhibit drinking behaviour. The factors that enter into this initial temporary satiation are probably numerous, and include the afferent activities initiated by the filling of the stomach. The 'distention' cue is only a part of the complex that enables the dog to judge the volume of water drunk, for even when deprived of this cue (esophagostomy) the dog does stop drinking. Without the distention cue, the other components of temporary satiation must overwork before drinking is inhibited; this results in overdrinking." (See also Bellows, 1939; Holmes & Gregersen, 1950). The cessation of drinking behaviour is thus governed by the reception of stimuli resulting from the behaviour, which may be proprioceptive or interoceptive.

In another sphere, Moynihan (1953) has shown that the incubation drive of the Black-headed Gull (*Larus ridibundus*) is satisfied only by "sitting on a full clutch of properly arranged eggs": if some of the eggs are removed, the stimulus situation is deficient and a displacement activity appears.(*) In this case the appropriate stimuli seem to be primarily exteroceptive.

A reduction in the tendency to perform a consummatory act caused by the perception of certain stimuli cannot be explained in terms of a theory which postulates "motivational impulses" which can only be discharged in action: these stimuli must have some sort of inhibitory effect on the centre. The observed fact is that *the perception of the appropriate stimuli leads to a reduction in the SAP of the behaviour in question.*†

However, although it is as yet too early to theorize on the manner in which the perceived stimuli produce this inhibitory effect, it must be emphasised that this inhibition of action by perceived stimuli is not incompatible with the main outlines of a hierarchical scheme. For instance, in the case of appetitive behaviour each releasing mechanism, in addition to being made sensitive to the appropriate stimuli by the activity of the functionally superordinated centre (see below), could inhibit that centre when the stimuli are perceived.

(*c*) **The nature of the Releasing Mechanism.**

In Tinbergen's scheme, the releasing mechanisms are regarded as "reflex-like"; they are presumed to be potentially active all the time, but only evoke responses when the appropriate centres are "loaded." This view is improbable not only on subjective grounds. Beach (1942c, 1947) showed that, although the latency of the response of intact male rats to females, the frequency of copulation and the rapidity with which ejaculation occurs is not materially altered by injections of androgen, the hormone "does exert a profound effect upon susceptibility to sexual arousal which is reflected in the increased variety of stimulus animals capable of evoking mating attempts." Similarly Prechtl (1953) has shown that, although the effect of a given stimulus in evoking begging in young Passerines does not alter with increasing hunger, the releasing mechanism becomes more and more unselective until finally normally quite inadequate stimuli become effective. This suggests that, with increasing motivation, the releasing mechanism becomes more active in the sense of becoming more unselective. It is thus clear that the releasing mechanism can not be described as "reflex-like" in any limited sense of the word reflex.

Another consequence of an analogy involving the flow of motivational impulses which are dammed up by a "block" below the centre is that a distinction between the stimulating and releasing effects of sensory stimuli becomes necessary. Thus, on Tinbergen's analogy, the stimuli may either increase the loading of the centre with "motivational impulses," or remove the block and permit these impulses to flow away in action. The basis for such a distinction is, however, by no means well established. Those stimuli which are often regarded as motivating (e.g. hunger pangs) may release appetitive behaviour (looking for food). Further, many stimuli have both releasing and stimulating functions. Thus van Iersel (1953) found that stimuli from the eggs not only release fanning in the Three-spined Stickleback, but activate the drive as well. Hinde (in press) found that, with those stimuli which were most effective in evoking the mobbing response of Chaffinches, the initial period of "warming up" continued for longer than with less effective stimuli; there were also indications that the response died away

* See also Bastock, Morris & Moynihan (1953). Some comments on conflict and thwarting in animals. *Behaviour*, **6**, 66-84.

† Cf. the recent paper by Deutsch (1953). A new type of Behaviour Theory. *Brit. J. Psychol.*, **44**, 304-317.

more slowly with the more effective stimuli. If the stimuli were merely releasing, the opposite effects might be expected. Similarly, experiments by Danziger (1951) show that, when rats have had experience of eating in a certain situation, that situation may be able to arouse a tendency to eat in the satiated animal, and acts like "an internally aroused drive." Danziger quotes a number of studies leading to similar conclusions. Such experiments seem to indicate that the distinction between releasing and stimulating stimuli is at least not so clear-cut as implied by Tinbergen's scheme.

The distinction between releasing and stimulating effects, however, seems to have arisen from the type of block which was pictured. Tinbergen clearly intended the "block" to be regarded as a functional one only, and if we dispense with the "flowing" "motivational impulses" a structural one "below" the centre need not be postulated. A number of other possibilities are open. It could be that the innate releasing mechanism has a normal inhibitory effect which, under the influence of the appropriate stimuli, is changed into an excitatory one. Or perhaps, when the appropriate stimuli are not present, the efferent discharge is continuous but is not co-ordinated or channelled—an explanation along these lines might be fruitful in the understanding of displacement activities and "irrelevant drives." As yet there is no evidence to decide between these possibilities, and if we adhere rigidly to a purely functional conception of the block, there seems to be no need to discriminate between the releasing and motivating effects of stimuli.

6. Long-term Effects of Experience on the Characteristics of the Mechanism

It seems worth while to emphasise that the performance of an activity may produce not merely a temporary lowering of responsiveness, but long-term changes in the characteristics of the central nervous mechanisms. Although such changes produced as a result of the previous experience of the individual concerned (excluding, of course, changes in stimulus-response relationships which are usually included in learning studies) have been investigated in only a very few cases, the results are sufficiently striking to indicate that they may be of much greater significance than is commonly supposed. Thus Beach (1948) has shown that mating behaviour often survives castration in sexually experienced adult male animals, but is always slight in the prepuberally castrated male. Elsewhere the same author has stressed the importance of experiences encountered in the first complete sexual contact on subsequent responsiveness (1947). Beach (1942b) also found that elimination of any two of the senses of olfaction, vision and cutaneous sensivity in the snout and lips eliminated mating in rats without previous sexual experience, but not in experienced animals. He regards this as due to a lowering of the copulatory threshold as a result of previous experience. Kagan & Beach (1953) showed that young rats kept in isolation for most of the time, but allowed contact with other individuals for short periods, learnt only to play with other members of the species. Such individuals were inferior in subsequent mating tests, apparently because of interference of the playing response.

Other authors have demonstrated a similar effect of early experience in other instincts. Mice with fighting experience remain aggressive for considerable periods after castration, whereas mice with no previous experience of fighting do not. Although there seems to be some doubt as to the nature of the effect of infantile food deprivation on the adult hoarding behaviour of the rat (compare Albino & Long, 1951, with McKelvey & Marx, 1951), Marx (1950) has presented an apparently plausible scheme whereby the behaviour itself may have been integrated by learning from its simpler components. Hall & Whiteman (1951) found that mice subjected to intense auditory stimulation in infancy were more "emotionally unstable" than the controls. Marx (1952) also found that rats which had learnt to eat rapidly in infancy retained the habit when adult (see also Ghent, 1951).

7. Discussion

The considerations advanced in the previous sections show not only that a theory invoking the flow and storage of "motivational impulses" is unnecessary, but that it leads to further assumptions which are incompatible with the data. A treatment of motivation in terms of a more operational concept, such as SAP, is to be preferred. It must be emphasised, however, that the differences from Tinbergen's scheme which have been stressed in the preceding section lie only in details. Tinbergen himself described these details as being "no more than a working hypothesis of a type that helps to put our thoughts in order." The

analysis of the evidence relevant to the hierarchical organisation of behaviour presented in Section 4 shows that the main structure of Tinbergen's scheme does not depend on the concept of flowing "motivational impulses," and that it provides an invaluable starting point for the study of the behaviour of the whole animal.

The use of the concept of SAP has been sufficiently exemplified in the preceding pages; it would as yet be premature to attempt a precise operational definition. This must await further investigation into:

(*a*) The relations between the possible criteria to be used. There are a number of possible observable criteria which might be used in the measurement of SAP—e.g. the strength of the stimulus required to release a response of given intensity, the intensity of the response to a given stimulus, latency, etc. Preliminary observations on the mobbing response given by Chaffinches to owls, however, indicate that the correlations between these different measures may not be high. Similarly Beach & Holz-Tucker (1949) found that various possible criteria for measuring the sex drive of male rats gave different values for the androgen dosage necessary to maintain the performance of castrates at the pre-operative level, and suggest the need for a combined score incorporating various measures. Further, detailed studies of a number of learnt responses (Hall & Kobrick, 1952) have shown a similar lack of correlation between the various possible criteria for measuring the response.

(*b*) The number of processes which underlie a change in responsiveness to a given stimulus. For instance, there seem to be *at least* four types of response decrement:

(i) Changes in responsiveness which are specific to the response but not to the eliciting stimulus: recovery is at least moderately rapid. Thus, the waning of the response of Chaffinches to owls involves also a decreased responsiveness to other predators such as stoats and snakes (Hinde, in press). The IR (Hull, 1943) component in the extinction of conditioned responses also has these characteristics.

(ii) Changes in responsiveness which are specific to the stimulus and from which recovery is fairly rapid. (See Prechtl, 1953; Glanzer, 1953; quoted on p. 47 of the present paper).

(iii) Changes in responsiveness which are specific to the response and from which recovery is extremely slow or absent ("instinctive regression", see Thorpe, 1951b; some cases of forgetting).

(iv) Changes in responsiveness which are specific to the stimulus situation and from which recovery is extremely slow or absent (Habituation, see e.g. Thorpe, 1951b; the sIR (Hull, *l.c.*) component in the extinction of conditioned reflexes).

In each of these cases the word "specific" is to be interpreted to allow for the occurrence of stimulus and response generalisation. Further, the terms "rapid" and "slow" recovery are relative: the actual rates of recovery no doubt vary greatly with the complexity of the response. The categories, are, of course, for the moment only convenient working ones—much work remains to be done on the relations between them, the various processes which produce increments in responsiveness, and the changes in responsiveness which occur in more and less complex patterns (e.g. spinal reflexes, Prosser & Hunter, 1936; Lehner, 1941). A study of these characteristics of the alterations in responsiveness may, however, give a clue to the stage in the neural mechanisms at which the correlated neurophysiological changes are occurring.

As an example of the sort of complication which is to be expected with more complex responses, the work of Grice & Reynolds (1952) may be cited. These authors found that, in a task learnt by human subjects on a pursuit rotor, there was a reminiscence gain during a rest interval even if the subject changed hands during the rest. They therefore suggest "the presence of temporary inhibiting factors either associated with generalised postural adjustment or of a perceptual or central character," but not localised in the specific effector system. The reminiscence gain was, however, smaller for the group which changed hands than for the group which did not, presumably indicating the presence of some inhibitory factors which were specific to the effector. Similar results were obtained by Irion & Gustafson (1952). The relationship of this type of response decrement to the categories given above is still to be worked out.

It is clear, however, that a given change in responsiveness may be due to a number of different processes and careful analysis is necessary to discover the role of each. Therefore, although the term SAP was originally

suggested as a successor to Lorenz's "reaction specific energy," it can be more usefully employed as a measure of the potentiality or readiness of the whole animal for response to a given stimulus. When the nature of increments or decrements in SAP are known, they can be described according to their properties (Response specific, Stimulus specific, Long-term, etc.). Such a use of the term SAP is still in accordance with Thorpe's definition, which refers to "The state of the animal responsible for its readiness . . ." (see p. 43). Further, it will help to emphasise the similarities and differences between responses in which the inborn component is conspicuous, and the learnt responses studied by Hullian and other psychologists: in its application, though not in the theory underlying it, the term SAP has much in common with Hull's "Effective Reaction Potential".

Summary

1. A constant stimulus presented at intervals to an animal does not evoke a constant response. It is thus necessary to postulate changes in the internal state.

2. These changes in responsiveness could be due to changes in the nervous mechanism underlying the response, or to changes in internal but extra-neural factors. Abundant evidence indicates that the former are the more immediately important.

3. The analogies of "reaction specific energy" and "flowing" "motivational impulses" used by Lorenz and Tinbergen to describe these changes are considered. It is considered that the concept of Specific Action Potentiality (SAP) (see Thorpe, 1951a) is likely to have certain advantages over them.

4. The evidence for Tinbergen's theory of the hierarchical organisation of behaviour is cosidered very briefly. The main outlines of the theory are well supported by observational and experimental evidence, but the "motivational impulses" model seems to lead to a number of additional assumptions.

5. These additional assumptions are considered in the light of recent experiments. In particular, studies are cited to show that a decrement in responsiveness may be related to the perception of a stimulus and not to the performance of an activity; that the releasing mechanism is not reflex-like; and that the distinction between the releasing and motivating effects of stimuli necessitated by Tinbergen's scheme is not supported by the evidence available at present.

6. Some studies are cited to show that the performance of a response may produce long term changes in the characteristics of the mechanisms involved.

7. It is suggested that changes in responsiveness are best described with the aid of the term SAP. Where known, the nature of the changes can be described according to their properties (Response specific, Stimulus specific, Long-term, etc.).

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Observations on the Grazing Behaviour of Different Breeds of Sheep at Pantyrhuad Farm, Carmarthenshire

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During rotational grazing experiments at Pantyrhuad* in Carmarthenshire during the summer of 1947, the opportunity was taken to carry out preliminary investigations of the grazing habits and behaviour of sheep. Four sheep of different breeds, viz. Suffolk, Spanish, Clun Forest and Scottish Blackface, were segregated from the main flock and observed continually for two separate periods of 24 hours each. At the time of the observations all the ewes were nursing single lambs which were (approximately) 3-3½ months of age. Different breeds of sheep were chosen in order that they could easily be distinguished when viewed from a distance. The observations during darkness were made with the aid of an electric torch in such a way as to disturb the sheep as little as possible.

The watches were carried out on a shift basis —four hours on and four off. Two observers were on duty at any one time, one to observe the animals through binoculars and the other to write down notes and plot the positions and movements of the animals. A record was kept of the actual occupation of each animal, i.e., time spent grazing, standing cudding, lying cudding, lying, and, also, the number of egestions urinations, sucklings and the number of times the sheep got up and lay down.

The first period of observation consisted of the 24 hours beginning 8 a.m. on 24th. June, 1947. The four ewes along with their lambs were put onto one of the plots (1.9 acres in area) and allowed a two-day acclimatisation period before the observations commenced, in order that the behaviour of the sheep would not be affected by the abnormal management. The plot offered abundant herbage; it had not been grazed since 7th. June. The second period of observation extended from 8 a.m. on 27th. June to the same time on the following day. During this period the same sheep were observed on another plot of similar size. This plot was fairly bare as the main flock had only been removed two days previously. The sheep were again allowed a two-day "acclimatisation period." The object of the change of plot was to enable a comparison of the behaviour of the same sheep to be made on pasture yielding different quantities of herbage.

To obtain an estimate of the distance travelled by each sheep during each 24-hour period, the plots were marked out geometrically by means of numbered posts; thus, the positions and movements of the animals could be plotted on graph paper and, later, an estimate of the distance travelled calculated.

Table I shows the time spent on each performance during the two 24-hour periods.

On the first day the average time per sheep spent grazing was 9 hours 36 minutes or 40 per cent. of the total time available, whilst on the bare pasture this time showed a considerable increase, the grazing time being 12 hours 11 minutes or 50.7 per cent. of the total time available. This increase was probably due to the grazing being much more selective on the second occasion. Most of the grazing took place during the hours of daylight, although, as shown in Table II, a higher percentage of the total grazing time was done between 10 p.m. and 8 a.m. on the bare pasture than was so on the good pasture, the figures being 5.2 per cent. and 24.3 per cent. respectively.

Table II shows also the time spent on each performance from 10 p.m. to 8 a.m. expressed as a percentage of the total time spent on each performance during the 24-hour periods.

From only two periods of 24-hour observation it is difficult to state with any degree of certainty the period of the day preferred for grazing, but on both occasions the sheep grazed for 45 to 50 minutes between 8 a.m. and 10 a.m.,

* An experimental farm of the Department of Animal Health, University College of Wales, Aberystwyth.

TABLE I. Time Spent on each Performance during the Two 24-hour Periods.
1st. Day — 24th June.

Ewe	Grazing	Standing Cudding	Lying Cudding	Standing	Lying
Blackface	9 hr. 18 min.	—	10 hr. 17 min.	58 min.	3 hr. 27 min.
Clun	9 hr. 47 min.	9 min.	10 hr. 11 min.	38 min.	3 hr. 15 min.
Spanish	10 hr. 24 min.	6 min.	8 hr. 43 min.	2 hr. 13 min.	2 hr. 34 min.
Suffolk	8 hr. 53 min.	20 min.	9 hr. 51 min.	59 min.	3 hr. 57 min.
Average	9 hr. 36 min.	9 min.	9 hr. 46 min.	1 hr. 12 min.	3 hr. 18 min.

2nd. Day — 27th. June

Ewe	Grazing	Standing Cudding	Lying Cudding	Standing	Lying
Blackface	13 hr. 11 min.	1 hr. 1 min.	7 hr. 12 min.	17 min.	2 hr. 19 min.
Clun	12 hr. 38 min.	3 hr. 18 min.	2 hr. 14 min.	4 hr. 20 min.	1 hr. 30 min.
Spanish	12 hr. 11 min.	6 hr. 35 min.	1 hr. 23 min.	2 hr. 21 min.	1 hr. 30 min.
Suffolk	10 hr. 43 min.	3 hr. 50 min.	5 hr. 20 min.	52 min.	3 hr. 15 min.
Average	12 hr. 11 min.	3 hr. 41 min.	4 hr. 2 min.	1 hr. 58 min.	2 hr. 8 min.

N.B. The time spent grazing includes the time spent walking around in search of suitable food.

TABLE II. Time Spent on each Performance between 10 p.m. and 8 a.m. D.B.S.T. (Average for 4 Sheep).

Performance	24th. June		27th. June	
	Time	Percentage	Time	Percentage
Grazing	30 min.	5.2	2 hr. 57.5 min.	24.3
Standing Cudding	5 min.	55.6	2 hr. 2 min.	55.3
Lying Cudding	6 hr. 9 min.	63.0	2 hr. 39 min.	65.8
Standing	56.5 min.	78.5	1 hr. 15 min.	63.6
Lying	2 hr. 19.5 min.	70.5	1 hr. 6.5 min.	52.0

there was a fairly intensive grazing period between 1 p.m. and 3 p.m. followed by another short period of approximately 45 minutes between 4 p.m. and 5.30 p.m.; the longest stretch of grazing took place during the evening when the sheep grazed almost continuously between 6.30 p.m. and 10.30 p.m. The latter period was interrupted by short periods of standing. It must be pointed out that the times given are for D.B.S.T. (Double British Summer Time). On the good pasture no grazing was done by any of the sheep between 10.40 p.m. and 8 a.m. the following morning, but on the bare pasture grazing continued until 11.15 p.m. and was followed by another period of grazing between 6.15 a.m. and 8 a.m. These observations were confirmed in a general way by observation of the sheep grazing the neighbouring plots.

It was noticed that the sheep grazed the short leafy herbage, and only occasionally were they observed to nibble the stem and inflorexence of a plant.

It was often extremely difficult during darkness to ascertain whether an animal was ruminating or not without disturbing the animal unduly; this fact may, therefore, in some measure account for the considerable difference in the total time spent ruminating over the two periods of observation. During the first period of observation the animals ruminated for 9 hours 55 minutes (average for four sheep), whilst during the second period the animals ruminated for only 7 hours 43 minutes. On the first day practically all the ruminating was done whilst the animals were lying down; only 9 minutes were spent ruminating whilst standing. On the second day the time spent ruminating was almost equally divided between ruminating whilst lying down and ruminating whilst standing, the actual figures being 242 minutes and 221 minutes respectively. The greater time spent ruminating whilst standing up on the second occasion was probably due to climatic conditions. It was observed that during heavy showers of rain, which were frequent on the second day, the sheep would stop grazing and, if lying down, would get up and stand facing away from the direction of the wind and rain; during such times the sheep would often ruminate and continue to do so for sometime after the rain had ceased. This observation was confirmed by general observation of sheep in the adjoining plots. It is interesting to note the very striking difference between the Scottish Blackface ewe and the Spanish ewe, the former, on the second day spent 432 minutes ruminating whilst lying down and only 61 minutes ruminating whilst standing up, the latter, during the same period, spent only 83 minutes ruminating whilst lying down and 395 minutes ruminating whilst standing up. From this observation it would appear that the mountain ewe is less affected by adverse climatic conditions, but, before any conclusions can be drawn on this point, further observations would have to be carried out on these breeds of sheep under conditions approaching those existing at Pantyrhuad during the second period of observation.

The night was preferred for chewing the cud when lying down; of the total time spent on that performance during the 24-hour periods, 63 per cent. on the first occasion and 65.8 per cent. on the second occasion took place between 10 p.m. and 8 a.m. During both periods of observation a little over 50 per cent. of the total time spent chewing the cud when standing up occurred between 10 p.m. and 8 a.m. During the hours of daylight the sheep ruminated for short periods (30-45 minutes) after a spell of grazing, the weather appearing to determine whether this was done when the animal was lying down or standing up.

The average total time the animals were completely idle (i.e. either standing up not chewing cud, or lying down not chewing cud) was 270 minutes on the first day and 246 minutes on the second day. During the first period of observation 73.3 per cent. of the total idle period took place when the sheep were lying down, whilst during the second period of observation only 52.0 per cent. of the total "idle period" was spent lying down. This difference was probably due to climatic conditions, since, as stated earlier, the sheep stood up during heavy rain showers. It can be seen from the previous table that the greater proportion of the completely idle period took place between 10 p.m. and 8 a.m.

During the first 24-hour period of observation the sheep were resting (i.e. lying down or lying down chewing cud) for an average of 13 hours 4 minutes per sheep; during the second day the sheep rested for only 6 hours 10 minutes per sheep. The period of rest was divided up into short intervals by the sheep getting up and then lying down again. The number of times each sheep lay down and rose again is shown in Table III.

TABLE III

Number of Times each Sheep Lay Down and Rose Again

Ewe	1st Day	2nd Day
Blackface	15	9
Clun	10	8
Spanish	9	6
Suffolk	9	9
Average	10.75	8.00

The period of rest during the hours of darkness were interrupted three or four times by the sheep getting up and lying down again within two or three minutes. It was observed that the sheep usually egested and/or urinated during these periods; sometimes the sheep got up and then lay down facing in a different direction, without apparently urinating or egesting.

A record of the total number of urinations and egestions during each of the 24-hour periods was kept and is shown in Table IV.

TABLE IV

Number of Egestions and Urinations

Ewe	1st Day		2nd Day	
	Egest-ions	Urina-tions	Egest-ions.	Urina-tions
Black face	8	12	7	13
Clun	9	7	7	11
Spanish	6	8	6	12
Suffolk	7	9	8	11
Average	7.5	9.0	7.00	11.75

From the observations it appeared that the sheep urinated and egested at any time during the 24-hour period.

During the observations, the rate of grazing was recorded over a series of separate minutes with the aid of a stop watch. The rates of grazing appeared to vary between 50 and 85 bites per minute, with an average of 70 bites per minute. During spells of very intensive grazing the rate was 75 to 85 bites per minute.

The rate of cudding was recorded. The average number of chews per bolus was 65, with 5 to 7 seconds between the swallowing of one bolus and the regurgitation of the next. The rate of cudding varied between 86 and 115 cuds per minute, with the majority of the recordings around 100 cuds per minute.

Distance Travelled by the Sheep

An estimate of the total distance travelled by each sheep during both 24-hour periods of observation was made by the method already outlined. The figures obtained are given in Table V.

On the pasture offering abundant herbage the sheep travelled an average distance of 2,037 yards (1.16 miles), but on the bare pasture the average distance travelled showed a marked increase up to 3,696 yards (2.10 miles). It will be seen from this table that the Scotch Blackface ewe on both occasions travelled less than any of the other ewes; this may to some extent be due to the fact that she developed a slight attack of foot-rot during the first period of observation, but it was also noticed that this

TABLE V

Total distance (in yards) travelled by each sheep during 24-hour periods

Ewe	1st Day	2nd Day
Blackface	1,558	2,888
Clun	2,268	3,772
Spanish	2,400	3,876
Suffolk	1,922	4,248
Average	2,037	3,696

ewe did not walk as far as the others whilst grazing, i.e., her grazing did not appear so selective. The much greater distance travelled by the ewes whilst grazing the bare pasture is most likely due to the grazing being much more selective, the increase in the distance travelled coinciding with an increase in the total time spent grazing.

The amount of herbage on the plots during the observational periods was estimated by cutting 40 sq. yd.-areas selected at random. The pasture yields were as follows :
June 24th.—Plot yielded 540 lb. D.M. per acre.
June 27th.—Plot yielded 143 lb. D.M. per acre.

The sheep did not travel far during the hours of darkness; the actual distance during this period appears to be influenced by the amount of herbage offering on the pasture, as is shown in Table VI.

TABLE VI

Distance (in yards) Travelled by the Sheep from 10 p.m. to 8 a.m. D.B.S.T.

Ewe	1st Day	2nd Day
Blackface	276	580
Clun	236	844
Spanish	292	436
Suffolk	398	852
Average	300	678

During the first period of observation only 14.7 per cent. of the total distance travelled during the 24 hours was done between 10 p.m. and 8 a.m. The same figure for the second period of observation was 18.1 per cent. On

neither occasion did the sheep travel at all between midnight and 5 a.m.

Summary

Observations are recorded on the grazing behaviour of a Suffolk, a Spanish, a Clun Forest, and a Scottish Blackface sheep over two separate periods, each of 24 hours. Data are recorded for the times spent in grazing, cudding, standing and lying, for the number of times each animal lay down, for the number of urinations and defaecations, and for the distances travelled.

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Grazing Behaviour and Helminthic Disease

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One of the outstanding peculiarities of helminth parasites is their inability to give rise to successive generation in one and the same host, every individual helminth requiring to spend part of its existence either as a free-living animal or as a parasite in some alternative host. Grazing animals are parasitised by a large group of strongyloid nematodes the infective stages of which are acquired while the host animal is grazing, so that peculiarities of grazing behaviour are capable of exercising a marked influence over the extent to which the animal will become infected with the worms.

The diet of grazing animals when confined to small fields and restricted pasture, as they usually are, may reasonably be regarded as a disgusting mixture of food and faeces such as to make the medical hygienists hold up their hands in horror and ask in amazement how these animals ever escape disease. It is not surprising, therefore, to find that some animals have acquired an abhorrence of faeces as part of their adaptation to life in a wormy world. The most obvious of these are manifested by equines and by bovines.

Although some more or less casual mention of these habits has appeared in print, no one as yet appears to have made them a primary object of investigation. The hygienic instinct of the horse becomes very obvious where a piece of grass land has been much grazed by horses alone. Such a field presents an alternation of long rank herbage where the horses defaecate but do not feed, and closely grazed parts where they feed but do not defaecate. A grazing animal may sometimes be observed to cease grazing and walk a considerable distance to defaecate in a rough part of the field. (It has even been suggested to me that thorough-breds show a greater degree of nice feeling about this sort of thing than do animals of less aristocratic lineage, and that even among thoroughbreds there is a marked difference between various families). The relative areas of the short and the long grass in different fields seem to vary with the concentration of the grazing, the extent of the grazed area being greatest where there are most horses. If cattle and sheep graze over the same ground, however, the rough grass is eaten off, and under those conditions I believe that the horses defaecate indiscriminately in any part of the field.

It is difficult to say how this separation into grazed and ungrazed areas first begins to take shape. I can only suggest that some instinctive equine preferences initiate the merest tendency to graze in some particular part of the field and to defaecate in another, and that presence of faeces in the one part and absence in the other provide the circumstances for the operation of more definite instincts. As a result of the continued growth of grass in the one part and its continual cropping in the other, a field then takes on the patchy pattern already referred to.

The pattern of a field much grazed by cattle is different, in that small patches of more or less rank grass may be seen evenly distributed over the whole surface. This may be regarded as evidence of a feeling of disgust at the association of their own faeces with food, but it represents a very inferior order of adaptation to crowded grazing conditions as compared with that of horses, there being no trace of instinct for the division of the field into dining room and lavatory.

The effect on these behaviours under our man-made conditions of intensive grazing is not wholely good, for while the intake of infective nematode larvae certainly tends to be reduced (and very greatly so in the instance of the horse) limitations are also placed on the intake of nutriment and sometimes to a dangerous degree. This is very noticeable where rich pasture has been intensely grazed by cattle. Such a pasture presents a very close studding with tufts of long herbage which not only greatly reduces the area available for grazing but undoubtedly takes away the fresh attractiveness of the food over the whole of the field to such an extent that the nutritional condition of the cattle is finally impaired. As the defence of grazing animals to parasitism depends to no small degree upon the resistance of a healthy and well-nourished body, the partial starvation to which this instinct

leads may culminate in helminthic disease.

One further point concerning horses is the observation that while the healthy adults abhor the faeces of their own kind, foals, during the first few weeks of their lives, show a marked tendency to eat a considerable amount of the fresh faeces of adult horses. This was observed during the course of a survey on the parasites of thoroughbred horses of all ages, from the date of birth. In this survey, the faeces of foals were found to contain not inconsiderable numbers of undeveloped strongyloid eggs, the presence of which could only be explained as a result of the eating of fresh faeces of infected adult horses by the foals. We supposed this to be some instinctive provision for the acquisition of the proper bacterial flora for the foals' intestines.

Casual observations in this field have not revealed any particular coprophobia on the part of sheep, a circumstance which might have some reference to what we may suppose to have been the sparse conditions of mountain grazing of primitive wild sheep in contrast to the crowded grazing of the more fertile lowlands by herds of wild horses and wild cattle. The well known high selectivity of grazing sheep, however, is an aspect of their behaviour that may play an interesting part in the development of parasitic disease in that they may tend to select in some instances, or to avoid in others, certain types of herbage that carry most of the helminth larvae. For instance, it has been shown that as a result of their respective conformations the trifoliate leaf of clover is likely to carry many strongyle larvae, while the upper leaves of grasses are relatively free. In selecting the clover leaves therefore the sheep would be collecting most of the nematode larvae.

Yet another point concerning sheep is the preference which they may develop, in certain extensive areas, for restricted patches of better grazing. This sometimes occurs as a natural consequence of some mild tendency for sheep to frequent a certain part of an extensive downland pasture. Through the more concentrated manuring of that part, the closer grazing, and the better trampling, the herbage becomes greatly improved and in the end the sheep spend a very large proportion of their time there, the result being a condition of overcrowding within a large area that makes ample provision for extensive grazing; as a result of this sheep become a prey to parasitism. A similar condition is brought about through the improvement of any small area of a mountain side, or of a prairie, either by localised manuring, or by reseeding.

Finally, the operation of grazing behaviour may be seen in the development of fascioliasis, both in the kinds of animals that are usually affected and in the season of the year at which the disease usually appears. The infective cysts of the liver fluke swim out of the carrier snails and get on to the herbage only in the wet kind of place in which these snails live. Horses do not like grazing the long herbage in wet places so that they very rarely sufferf rom fascioliasis; the same preference for dryer places applies to sheep and to cattle although not to such a marked degree. During the spring, while there is plenty of herbage elsewhere, the wet places are not grazed and it is only towards the latter part of the summer, when places that were wet in the spring have dried out and when herbages elsewhere may have become scanty, that these animals go into ditches and into other snaily places and acquire the infective cercariae. This in large measure provides an explanation for the prevalence of fascioliasis during the winter months.

Johnstone Wallace has shown the disgust exhibited by cattle to be a matter of smell, since they will readily eat herbage which has been cut from the close proximity of deposits of faeces. A casual observation that I made on the grazing of goats, however, suggests that the taste of rank herbage may be the factor which repells these animals. Having noticed a number of tufts of long rank herbage in a paddock grazed by goats, and endeavouring to ascertain the reason, I found the remains of almost completely disintegrated goats' faeces at the centre of each tuft. In the proximity of more freshly passed faeces, however, the herbage had been eaten off quite cleanly suggesting that the goats were not repelled by the smell of faeces, at least not of faeces that were only a matter of some days old, that perhaps they were not repelled by the faeces at all but only avoided the rank grass that happened to be growing around the stale faeces.

There can be no doubt that the collection of data on the grazing habits of pasturing animals would lead towards a better understanding of the epidemiology of parasitic disease.

The Clustering of Honeybees at a Food Source

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Introduction

Bees may cluster naturally during the swarming season and also under certain artificial conditions, for instance when they are confined in a green house or in a dark box (Lecomte, 1950, 1951).

Forel (1910) described how on several mornings he was driven from the breakfast table in his garden by great numbers of bees, which by formation of clusters and by fighting made a continuation of the meal impossible; v. Frisch (1914) reported that whenever he offered ample food to the bees for some time so many of them crowded the feeding place that observation of individual behaviour became impossible.

In the present paper this clustering on the feeding site, and in particular its social aspects, has been made the subject of investigation.

Description of a Cluster

Foragers collecting syrup fly for a while quietly to and fro between the dish and their hive. However, when their number increases above a certain value, a conspicuous change of behaviour occurs: the bees suddenly settle down in great numbers spilling over the dish and table. In the milling mass many bees do not get at the syrup and all are disturbed in drinking. Fighting often ensues and many foragers leave the site, but in spite of this, and although the syrup soon gets exhausted, a cluster may persist for minutes or even hours.

Quick cluster formation can be provoked by removing from a training table, during intensive but still orderly foraging, the syrup dish with the bees on it, until a large number of bees are hovering over the site, and then putting the dish into position again.

While certain changes in the behaviour of the bees at the time of the cluster formation (e.g. fighting and disturbance) indicate that interactions take place between the individuals, it is impossible to decide by simple observation whether the formation of a cluster itself is merely a result of the parallel attraction of the individual bees to the syrup dish or whether mutual attraction between the bees plays an important part. The following experiments demonstrate the existence of such mutual attraction and elucidate its nature to some extent.

Materials and Methods

A colony of Buckfast bees was placed in an orchard about one mile from the nearest apiary. A 'feeding table' of thick glass, 2 ft. × 5 ft. in size, was placed fifty yards away; on this the bees were trained either to Petri dishes containing sugar syrup or to 6 in. high cylindrical cages, made of perforated zinc with Petri dishes at top and bottom. Observations and counts were made after training, either on this feeding arrangement or on a similar 'clean' one.

Number of Bees Visiting 5 Dishes Containing Concentrated Syrup

Five dishes with 67% sugar syrup, arrayed in quincunx on the table, were offered to the bees with a view to observing their visiting behaviour. No bee found the dishes in four hours, so one bee was brought, and marked with red paint. After returning to the hive she paid two more unaccompanied visits to the same dish and then other bees appeared near the table searching for food. During the absence of the first bee a second one landed, after some hesitation, on another of the syrup dishes; she seemed attracted by one of the several wasps which had been visiting the dishes all the time, fell into the syrup and had to be destroyed. A third bee which arrived while the marked bee was drinking landed on the same dish, a fourth bee on another dish, and from then on the visiting population started to build up. Table I shows the number of visitors counted at two-minute intervals between the 9th and the 23rd minutes of this experiment, on each of the five dishes.

Table I indicates that the number of visitors on the various dishes very soon became significantly unequal and remained so for some time. Continued observation showed that when the syrup was used up in the most visited dishes 1 and 3, the other three dishes were eagerly visited, so they were not repellent.

Table I. Number of Bees on 5 Petri Dishes containing 67 per cent. Sugar Syrup

Minutes after the first visit	1st dish	2nd dish	3rd dish	4th dish	5th dish
9	4	—	1	—	—
11	3	2	—	—	1
13	7	1	—	—	1
15	14	—	1	—	—
17	25	2	6	—	—
19	40*	2	11	—	1
21	70*	1	19	—	3
23	100*	—	40*	—	1

* approximate numbers

Unequal numbers of bees visiting apparently similar dishes has variously been ascribed to differences in position, accessability, or other slight inequalities unconnected with the presence of bees. Such factors must in fact be held responsible for the choice of particular dishes by the first visitors, but the following experiments indicate that the rapid building up of great numbers of bees on a dish is caused by the attraction of bees for each other.

Cluster Formation by Trained Bees on Empty Dishes

By changing the position of 5 syrup-containing Petri dishes every two minutes several hundred bees were trained for one hour to visit them indiscriminately. Then the glass table with the dishes and the bees on them was carried 20 feet away and hidden under a tarpaulin; a similar clean table with five clean empty dishes was substituted in the original position. Soon about 100 bees were hovering over the site. After some hesitation a first bee settled in one of the dishes, five seconds later this dish contained seven bees and 10 seconds later 29 bees. At this time there was still no bee in any of the other four dishes. After one minute more than 100 bees were in the first visited dish, searching, bumping into each other and occasionally fighting in pairs or with a few wasps. In two other dishes were four bees and one bee respectively; the remaining two dishes were still empty. The clustering in the first visited dish lasted for 24 minutes, during which time numbers fluctuated between 16 and over 150 bees. Then for about two minutes no bee was visiting on the dish, but a small cluster formed again and lasted for another 3-4 minutes. In the other dishes the number of bees never rose over five and for long periods one or the other was quite empty. Thus there was gross inequality in the numbers of bees on the individual empty dishes.

In similar experiments of this type, as a rule only one cluster was initially formed, but if the dish or cage on which a cluster had formed was removed another cluster formed instantly on another empty dish or cage; this procedure could be repeated.

Changes in Behaviour During Cluster Formation

As long as the number of bees on any dish was small (under 5) peace reigned and the search for food was usually not very agitated. However, as soon as more bees had settled—frequently on top of each other—and when the cluster grew big enough to spill over the rim of the dish, angry searching and fighting ensued and at this stage the experimenter was stung several times. Closer observations also showed that the frequency of settling and the duration of individual visits under those conditions altered; a few measurements are presented in the form of a diagram (Fig. 1).

Fig. 1 shows the number of bees at various periods settling on an empty dish, as well as the frequency and duration of the visits of one individual bee, fed for the previous 25 minutes on concentrated (67%) syrup. The graph shows a rapid increase in the numbers of visitors, their maintenance for some time, and, finally, a gradual decline owing to dispersal. The visits of one particular marked forager were longest shortly after the beginning of the experiment, i.e. after the initial build up when numbers on the dish were high; visits shortened later on when the numbers of bees were small. A similar behaviour was observed in a subsequent experiment (Fig. 1, bottom) with the same flock of bees after feeding dilute syrup (17%) for another 25 minutes. A cluster formed again on an empty dish and the only differences were that the number of bees increased neither so rapidly nor to such a high level as in the first case, and that fewer and shorter visits were paid by a marked bee (a different one). In similar repeated experiments the intensity of visiting varied, but all can be summarized as follows:

1. Negative correlations of greatly varying

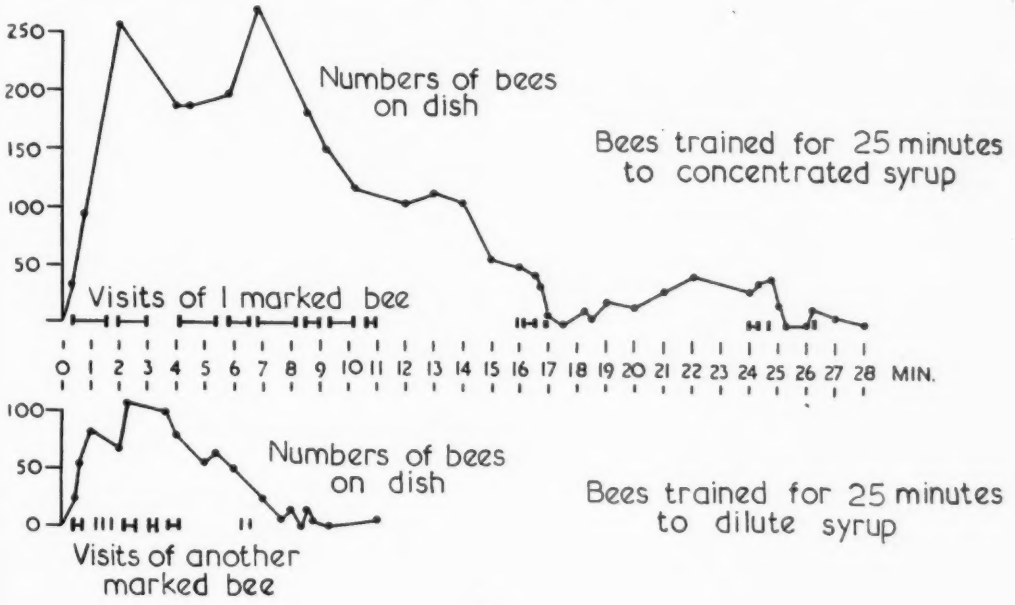
250
200
150
100
50
Numbers of bees on dish
Bees trained for 25 minutes to concentrated syrup
Visits of I marked bee
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 MIN.
100
50
0
Numbers of bees on dish
Bees trained for 25 minutes to dilute syrup
Visits of another marked bee

Fig. 1

magnitude were found between the time elapsed from the beginning of the observation and the number of bees on the dish ($r = -0.11$ to -0.90). 2. Negative correlations were found also between the time from the beginning of the experiment and the duration of individual visits. ($r = -0.35$ to -0.74). A strong positive correlation ($r = 0.50$ to 0.98) was found between the numbers of visitors and the duration of individual visits.

Demonstration of Mutual Attraction

While the demonstration of the positive correlation between the numbers of visitors and the duration of individual visits at any particular phase of cluster formation agrees with the assumption that the bees in the empty dish stimulate each other to prolonged searching, it cannot by itself prove this point. Nor can the greater frequency of visits be taken as proof of a stronger attraction by greater numbers, as both phenomena may be conceivably controlled by one and the same (non-social) factor. Proof of mutual attraction can only be provided by a demonstration of the attractivity of decoys (either whole bees or certain isolated features of bees).

Interactions of foragers on a *natural* crop are not usually manifest among honeybees. Although v. Frisch (1919) reported that bees trained to smells and entering closed feeding cages do not to any great extent follow each other, he observed that when the bees on the dishes could see each other there was a group attraction.

In the present experiments the learning of position was kept to a minimum by careful moving of dishes during the feeding, and attraction by a group of bees, or even by one single bee, was often quite conspicuous. It was, for instance, frequently observed that trained foragers coming from the hive settled directly on a bee drinking alone on a dish, although there was plenty of room in this dish and in several other dishes; quite frequently the first visitor was unsettled by this behaviour. Solitary searchers in an empty dish were also frequently pounced upon, although this behaviour usually gave the impression of an attack; under such conditions bees also settled on wasps and vice versa. It should be noted that, before cluster formation, successive encounters frequently occurred in different dishes, so that any special attraction to a particular dish can at best have lasted but a short time.

It is therefore reasonable to ascribe the landing in any particular encounter of the later visitor on the dish, on which the first had already settled, to an attraction of the second by the first. Assuming this conclusion to be correct, an attempt was made to isolate the stimuli responsible for this attraction (called 'social releasers' by Tinbergen, 1951).

Search was focussed on those perceptions which have been shown to influence bee behaviour in other ways, i.e. vision (v. Frisch, 1914) and smell (v. Frisch, 1919), which are effective in directing foragers to a source of food as well as to the perception of vibration which seems to be operative in sedentary bees (Hansson, 1951) and in particular in bee clusters in the dark (Lecomte: 1950, 1951).

A visual component in the mutual attraction was demonstrated in three ways:

1. By using living or dead bees as decoys under conditions which excluded olfactory attraction,

2. By using the mirror image of the visitors themselves for attraction,

3. By the use of silhouettes of bees.

Attraction by Bees Under Glass

In these experiments about 200 bees were fed 67% sugar syrup on five Petri dishes the positions of which on a table were changed 'cyclically' every two minutes. After 30 to 40 minutes the whole arrangement was replaced by a fresh table with five new empty dishes, which were all covered by one square sheet of glass 2 ft. × 2 ft. One of the dishes contained various numbers of living or killed bees, and it was observed whether the cluster formed over this particular dish or elsewhere. The bees trying to land on a dish often did not seem to notice the glass plate on top of the dishes, and bumped into it or landed in a clumsy way. Nevertheless, clusters formed rapidly.

Experiment on 21st. September, a warm and sunny day. After 30 minutes' training a fresh table with four empty dishes and one dish containing five living bees was placed into position; within 10 seconds a cluster formed on the glass plate on top of this dish. The new table was then quickly removed, the feeding table was put back into position and feeding was resumed for 10 minutes, during which period dish positions were changed five times. Then a second clean arrangement was offered with a dish containing five bees in a position different from that in the previous experiment. Again a cluster formed on top of the dish containing the five bees, and half a minute later a second cluster formed on a neighbouring dish. The experiment was repeated a third time and the bees again alighted on the top of the dish with the five bees. These were presumably *seen* by the trained foragers.

The experiment was then continued but the number of decoy bees in the dish was reduced to three. In five successive observations first clusters formed twice over the right dish and three times over one of the four empty dishes. In addition, two second clusters formed over the dish containing three bees. Thus, clusters formed in the correct place more often than might be expected by chance. One single bee probably exerts some visual attraction, but this would be tedious to prove by the above method.

In a further experiment, white paper discs were placed underneath the Petri dishes during feeding and during observation. In these conditions of stronger brightness contrast two captive bees were attractive four times out of four experiments, but one captive bee was missed twice in four trials.

Using the same technique some further experiments were performed in order to find out whether moving bees were visually more attractive than motionless (dead) bees. Such an effect was expected, as Wolf (1935) demonstrated that flicker attracts bees, but no significant difference of attraction due to movement could be established.

Attraction by Mirror Image

September 24th, overcast sky and mild.

About 300 bees were fed for 30 minutes on five Petri dishes with white paper discs underneath. On the 'clean' table a round mirror of similar diameter as the paper discs had been placed under one empty Petri dish while under the other four dishes were discs of white paper.

A few seconds after exposure of the clean table, while a cloud of bees hovered over the table a cluster formed in the empty dish over the mirror (Fig. 2). Four repetitions gave the same result. Thus, the group of bees was attracted by its own reflected image.

On the following day, when, owing to cold weather, fewer bees flew (Schuà, 1952), four out of a series of seven such experiments were

successful, but three were negative; this still indicates an attraction by the mirror. The decreased attraction by the mirror on this particular day may be explained either by the weather conditions directly, or by the fact that the smaller number of bees hovering over the mirror would make the image less attractive. The latter explanation would agree with the observation that a mirror did attract single searching bees.

Although mirror experiments of this type are fairly indicative of the existence of a visual stimulus they are not by themselves conclusive; the brightness and patterning of a dish on top of a mirror even under an overcast sky are invariably different from the brightness and pattern of a dish on top of a white paper disc and may in fact often be more attractive to *searching* foragers. On the other hand, the bees in the described experiments had been *trained* to paper discs and not to a mirror.

Experiments with Silhouettes

Six types of visual differences between bee models were provisionally (=qualitatively) explored in respect of their effect on cluster attraction: differences between spatial and flat models, differences between cut-out figures of different colours and shades, and differences of size, shapes and numbers.

The lay out and general procedure was the same as in the previous experiments. Discs of white paper the size of Petri dishes were placed under the five feeding dishes. When fresh empty dishes were offered, white paper discs were under four of these, while under the fifth was placed a similar disc on to which bee-like figures cut out of coloured paper had been glued. These were varied in respect of numbers, relative position, shape, colour and size. It was then noted, whether the 'first cluster' formed in the dish on top of the cut-out 'bees' or on any other dish.

The results were briefly as follows:

1. Models need not be tridimensional, as cut-out paper bees proved clearly attractive.

2. The colour and shape of these cut-out paper bees did not greatly matter, as long as they were fairly dark; this one might have expected from the experiments of Hertz (1933). Cut-out bees somewhat larger than real ones might even surpass the latter in their visual attraction; and black cut-outs showing a greater contrast to the light background than real bees might also be more attractive (Tinbergen's super-normal sign stimuli).

3. Clusters formed with certainty over the silhouettes of 12 and 8 bees if they were of normal size and dark brown in colour, but less certainly over four or one. Also, the greater the number of silhouettes, the quicker, on the whole, did a cluster form.

Summarizing the experiments with glass covered bees, with mirrors, and with cut-out bee silhouettes, it can be concluded that the visual image of bees in the conditions described attracts other bees and thus is a factor in cluster formation.

Olfactory Attraction

The odour released by the scent glands of a fanning bee is noticeable to man and attracts individual bees searching for food. Recently it has been shown (Kalmus & Ribbands, 1952) that colony-specific odours are used to make syrup dishes attractive to individual searchers of the same colony. A fainter 'body odour' of foragers, which may or may not be qualitatively distinct from the fanning odour, also attracts other bees.

In the following experiments the roles of fanning odour and body odour in respect of cluster formation were investigated and the odour intensity and persistence semi-quantitatively assessed. Cages or dishes were used.

Cage Experiments

Cages were made of perforated zinc with a Petri dish as bottom and another as top (Fig. 3); through a hole in the zinc, bees could be introduced into the cage. These, though audible when buzzing, were scarcely visible from the outside.

Bees were fed with syrup in the Petri dishes forming the top of five cages not containing any bees. After 40 minutes training, during which the position of the cages was systematically changed every two minutes, five fresh cages were offered on a fresh table, the tops of which did not contain any syrup, but one of which contained inside a varying number of freshly caught bees. It was observed whether a cluster formed on top or on the side of this cage, or—failing this—where the greatest number of searching foragers were hovering. These 'incomplete' reactions occurred because the bees were trained to settle on top of the cages, whereas the attractive scent from the caged bee, could

only emerge sideways through the perforated cylindrical wall. Clusters sometimes formed on the wall of a cage or—rarely—not at all, even when a majority of 'interested' bees were hovering around the 'right' cage or on the leeside in front of it (Fig. 3).

The results were as follows: as long as they did not fan, at least 15 bees had to be enclosed to attract noticeably greater numbers of hovering bees to a particular cage, and about 25 caged bees were necessary to ensure that the first cluster formed on this cage. If, however, fanning was provoked in a single captive bee either by feeding it with syrup or in any other way, strong attraction and rapid cluster formation could several times be observed. Thus, 'fanning odour' as well as 'body odour' can induce clustering, but the latter is a much less potent stimulus.

Experiments with Bee-scented Dishes

Attraction of individual bees, both trained and untrained, to a dish previously visited by other bees has been demonstrated (Kalmus & Ribbands, 1952). The following experiments show that the lingering scent of bees also induces clustering.

After feeding bees in the usual way for 30 minutes on five dishes containing concentrated syrup, one clean empty dish on a fresh table was put in place on the training table; a cluster formed immediately and between 20 and 50 bees were allowed to crawl over the dish for one minute. Then the bees were scattered and the empty dish removed. The table with the five syrup-containing dishes was again put into position and the bees fed for eight minutes, the dishes being moved four times. Meanwhile, on the clean table some distance away the 'scented' empty dish was placed between four other empty dishes; some straying bees tried to land on the scented dish but were chased away. When after the eight minutes the 'clean' arrangement was again moved into position, a large cluster immediately formed in the scented dish while the other four were not visited. The cluster-containing dish was emptied of bees and put in another place on the table, where again it was soon overflowing with bees. This procedure was twice repeated. In a third attempt a secondary cluster formed in a not-previously scented dish; the first scented dish was removed and the second visited dish, now scented, was used with four fresh dishes; it proved to be attractive.

To demonstrate the cumulative nature of scenting, bees were fed for half an hour in *nine* dishes and nine empty dishes were offered them for cluster formation. Of these, dish A had been visited by about 15 bees for 20 seconds, dish B by a similar number for one minute, dish C for 3 minutes and dish D for 5 minutes. (These visits were induced in the manner explained above, in the order A.B.C.D. The other five dishes were not visited). After a further 10 minutes' feeding on the nine syrup-containing dishes, all the nine empty dishes were offered to the bees; a cluster immediately formed on dish D. This was removed and the bees scattered. The next cluster formed in C, and the third in B. The fourth cluster formed in an unvisited dish, and the fifth one in dish A.

From this experiment which was repeated with a similar result, it was concluded that 15 bees searching an empty dish for 20 seconds probably left enough scent behind to attract a cluster, even after ten minutes. Moreover, an increase in visiting numbers, or in the duration of the visits, increased the attractiveness which was roughly proportional to the sum of the number of seconds spent by each bee in the dish.

Acoustic and Vibratory Stimuli

Hansson (1951) states that bees on the combs of a hive can react to sounds produced by the queen and to a wide frequency range of mechanical oscillations. Lecomte (1951) states that in his experiments vibrations produced by the bees contributed to cluster formation in a dark box. Acoustic reactions of individual bees during flight have been variously claimed and denied.

Two kinds of sound sources, both transmitted through a loudspeaker, were used in the following experiments:

1. Electronic oscillations of various frequencies and intensities, and

2. Recordings of the noise of bees visiting a dish.

Electronic Oscillations

An electronic audiofrequency wave generator attached via a volume control to a powerful loudspeaker of 12″ diameter (lowest frequency about 80 Hertz) was used to detect possible reactions of bees flying over the site. No effect whatever was observed with frequencies between 80 and 2,000 Hertz and, in particular, clusters did not form preferentially on empty

PLATE I

Fig. 2

Fig. 3

dishes which were placed on the horizontal membrane of the loudspeaker.

In one experiment however, when the loudspeaker was covered by a sheet of paper in a frame, it was observed that a few bees, which had accidentally settled on the paper, became stunned and motionless when it vibrated with a frequency of 200 Hertz, while they moved again when the vibration ceased. In subsequent experiments this effect could be observed more or less distinctly at frequencies between 80 and 1,500 Hertz, which well agrees with the observation of Hansson (1951). Thus, while an attraction of flying bees by sound could not be demonstrated, it is nevertheless possible that sound or vibration play some part in keeping settled bees in a cluster. This agrees with the conclusions drawn by Lecomte (1951).

Recording of Buzzing Sound

The sound of bees buzzing round a dish was recorded by a Ferrograph tape recorder. Played back, the recording sounded very natural and it could be greatly increased in intensity. However, when emanating from a small microphone inside one of a group of wire cages, the recording, whether played at natural intensity or much louder, had no observable effect whatever on bees flying in the neighbourhood and did not induce clustering.

Comparison of Visual and Olfactory Stimuli

In the absence of demonstrable acoustic effects during cluster formation only certain visual and olfactory stimuli could be compared in respect of their relative effectiveness on clustering.

In one series of experiments bees trained to five dishes were offered the choice of one scented dish, one dish with enclosed bees or silhouettes of bees, or of three empty dishes. During training and observation, white paper discs were placed under every dish.

The results of three such experiments were :

(*a*) The attraction of 8 black silhouettes was compared with that of the scent of 600 'bee seconds' (20 bees settled for 30 seconds) and it was found that the first cluster formed in the dish over the 8 silhouettes. When this was removed another cluster formed in the scented dish, and only after the removal of this dish was one of the three control dishes visited.

(*b*) The attraction of 10 living bees seen through a glass plate was compared with that of the scent left by about 20 bees in a minute (1,200 bee seconds) and another three empty Petri dishes. The first cluster again formed in the visually marked dish and after its removal the second cluster formed in the scented dish.

(*c*) A dish under which five bees could be seen proved less attractive than the scented dish used in the previous experiment.

Considering the impossibility of direct measurements of bee odour, no attempts were made to determine the relative efficacy of visual and olfactory attraction more accurately or under different conditions. While in the prevailing cool weather the sight of 5-10 bees was roughly equivalent to a scent of about 1,000 'bee seconds', there were indications that the olfactory attraction of the same number of bee seconds may be relatively greater on a warm summer day but less lasting. A corollary of the equivalence of different stimuli is the possibility of their summation. This was easily demonstrated for cluster formation: visual and olfactory stimuli were less powerfully attractive when offered separately than when offered jointly.

Cluster Formation on Alder Twigs

The following accidental observations may be of interest because they show that cluster formation can be directed by stimuli to which the individual bees concerned almost certainly have not been exposed.

The observations were made on the occasion of an unsuccessful attempt to prove the superiority of attraction of visual patterns in space as opposed to similar patterns in the plane. For this purpose three inch-long pieces of branches and twigs from an alder tree were put in various arrangements on the training table. Although the bees had been trained to syrup dishes, clusters formed immediately on a little stake built from nine twigs. This happened several times. Similar arrangements of twigs of other trees and bits of dry wood were on this particular day (September 19th) far less attractive, and on the next day the original alder twigs were also hardly visited. However, a stake from freshly broken twigs of the same tree immediately attracted a cluster, and when some bark was peeled off the twigs of the previous day's stake, bees clustered on these too; it seems that the combination of the strongly contrasting shades of the broken surface with the moisture and smell from the destroyed tissue is

particularly attractive to bees eager to settle.

Discussion

The results reported in this paper have a bearing on the collective and on the individual behaviour of foraging bees. The first point to consider is the nature of a bee cluster. In his classification of animal aggregations Allee (1931) contrasts the loose transitory associations of individuals from a normally solitary species with the stable societies of social organisms. The former arise as a rule from the parallel attraction to a particular locality of many individuals by one or several external stimuli, e.g. from optimal light or temperature conditions, and mutual attraction between the individuals is only of secondary importance to the group formation. On the other hand, interactions between individuals form the basis of stable animal societies and attractions of particular localities, other than those exerted by the individuals occupying those localities, do not play such a dominating role in such aggregations.

Now, while a colony of honeybees undoubtedly is a stable and highly integrated society, a transitory bee cluster may be thought to result from either parallel attractions of the training site or the mutual attraction of the bees or from a combination of both. In this paper it has been shown that visual and olfactory mutual attraction play a decisive role in inducing clustering on a feeding site. Clustering without previous training has been observed by Lecomte (1950), who studied the 'interattraction' of queenless workers contained in a dark wooden box. He found that the minimum number necessary to form a unique cluster was about 50 and that smaller numbers formed several small clusters or none at all. Cluster formation took between 75 and 195 minutes and was fairly independent of temperature. Lecomte concluded from some of his experiments that the bees attracted each other by odour emanating from the abdomen and possibly by vibratory stimuli of about 30 Hz. In a later paper Lecomte (1951) reported that, in the conditions stated, the attraction of 50 workers was about equivalent to that of one queen.

From Lecomte's and my experiments it can be concluded that cluster formation is a 'social activity'; the bees strive to be in the neighbourhood of fellow members of the species when performing their instinctive activities (Tinbergen, 1952).

It now remains to give an interpretation of the behaviour of the individual worker bees during the formation and existence of an experimental cluster. The experiments are possible through the habit of foraging. This urge to collect nectar or pollen may be considered a derivative of the ordinary striving after food of solitary animals and being an appetitive instinct it does not require any training. The settling of a bee on a dish, on the other hand, is an acquired habit the intensity of which depends on the intensity of a bee's training, the number of its disappointments (counter-training) and the sight and smell of other bees visiting the dish. Meteorological factors, foraging conditions and the general state of the colony may control the intensity of the innate foraging drive and thus indirectly the urge to settle on a dish. It might be asked whether the visual and olfactory properties of their fellow bees which have been shown in this paper to induce a bee to join a cluster are innate signals or merely ones which are associated with the presence of other bees during the training period. As it is impossible to rear bees in isolation this question can not be directly decided. The stimuli which lead untrained bees to flowers (Oettingen-Spielberg, 1948; Butler, 1951) are of the same nature as the stimuli to which bees can be trained.

Summary

Bees which were fed for some time on concentrated syrup settled on the feeding site in the absence of syrup and frequently formed a cluster. When several empty dishes were offered to trained bees they did not settle equally in all of them, nor independently from each other, but the earlier settled ones attracted later arrivals. Bees enclosed behind glass, silhouettes of bees and their own mirror image, or the odour left behind by previous visits, proved attractive. Mechanical vibrations seemed to help in keeping foragers settled in a cluster. With competing stimuli, the place of clustering was used as a criterion for their relative attractiveness.

Acknowledgements

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The Feeding Behaviour of Phosphorus-Deficient Cattle and Sheep

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Introduction

In 1924 Theiler, Green & du Toit described the perverted feeding behaviour of phosphorus deficient cattle and showed that either osteophagia and/or allotriophagia are normally signs of phosphorus deficiency. It has been suggested that when the deficiency is not severe the perversion of appetite, or pica, may not be obvious and may be limited to the chewing of clean, dry, sunbleached bones, a condition known as osteophagia. When the deficiency is serious, however, the pattern of the depraved appetite is more complex and the condition is known as allotriophagia. Green (1925) lists the following materials as being readily eaten by phosphorus-deficient animals but ignored by normal ones: bones, cinders, sacks, tins and "the weekly washing waving in the wind." As an example of severe pica, Green tells of an "extreme craver" which crunched a living tortoise. In the case of phosphorus-deficient sheep the condition is less apparent, but it is known to occur and has been demonstrated.

This peculiar feeding behaviour has often been quoted as an example of "nutritional wisdom" on the part of ruminants. Katz (1937), for example, argues that an animal's decision to eat bones is due to a subconscious but irresistible desire to restore its biochemical equilibrium by means of a high intake of phosphorus. It is obviously important from many points of view to know if the proposition, expressed in the colloquial phrase 'A little of what you fancy does you good', is nutritionally valid, and for this reason we undertook some observations upon the feeding behaviour of phosphorus-deficient cattle and sheep.

Two adjacent areas were located in Glen Brittle and Glen Drynoch in the Isle of Skye. The total area involved was approximately 5,500 acres of which only 85 acres were arable, the remainder being unimproved rough grazings. The stock grazing this area totalled 90 cattle and 500 sheep. Analyses of both soil and herbage which were made by the Macaulay Institute for Soil Research, confirmed that the grazings were seriously lacking in phosphorus, and showed that there were low to adequate levels of calcium but no deficiency of trace elements. The grazing supplied, also quantitatively,enough food on offer. Blood samples were collected from a number of cattle in the Glen Brittle region and the inorganic phosphorus levels were determined by the Veterinary Investigation Laboratory, Mill of Craibstone, Bucksburn, Aberdeenshire. Results from these analyses were uniformly low, ranging between 1.8 and 2.5 mg. of inorganic phosphorus per 100 ml. of blood, whereas in an adequately nourished animal the level is of the order of 5.0 mg. (Theiler & Green, 1932). Finally, it was known that the cattle on these grazings showed obvious allotriophagia and therefore the locality provided highly suitable conditions for this investigation.

Methods

We offered the grazing animals a choice of suitable mineral supplements and observed the extent to which they showed a preference for the one containing phosphorus. Eight groups of three troughs in each were dispersed over the area, six groups in Glen Drynoch and two in Glen Brittle. In each group two troughs contained only calcium carbonate (ground limestone) but the third contained a mixture of equal parts of calcium carbonate and dicalcium phosphate. The troughs were specially designed to present the same area of mineral supplement to the animals and each trough contained more than enough of this to last for the duration of the experiment. Precautions were taken

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also to ensure that the minerals were well protected from the weather while at the same time they were readily accessible to the animals. Undoubtedly a very little material was blown away but the high humidity of the locality caused the powdered substances to become moist and set firm in a few days and therefore these losses were not great. Undoubtedly almost all of the material removed from the troughs was actually eaten by the animals on the grazing. The latter were seen to investigate and sample the trough contents. Records were made of the amounts of material removed from each trough from April, 1951, to November, 1951, and from November, 1951, until the experiment ended in March, 1952.

Results

From Table I it will be seen that the mean food consumption from each trough containing phosphate was 69 pounds dry matter, while that from each trough containing only calcium carbonate was 46 pounds. A statistical analysis, taking into account the variability of intake from different troughs containing the same supplement, showed that this difference is not significant at the 5 per cent. level. The possible influence of the position of each trough in respect to the others in the same group on the selection of the supplements was investigated and found to be negligible. These results therefore indicate that there is no specific urge on the part of phosphorus-deficient animals to eat food containing phosphorus. Indeed it appears that the minerals were eaten either for the calcium content or merely as part of the general pica.

Table II. gives the phosphorus intake of each cow expressed as P_2O_5.

The very low figures for daily intake per cow are markedly below the intake necessary to prevent aphosphorosis in cattle grazing deficient herbage, about O.5 oz. (15 g.) P_2O_5 per dry cow per day (Beeson, Bolin, Hickman & Johnson, 1941). The 500 sheep on the grazings, the daily phosphorus requirement of each of which would

TABLE I. Showing the Amounts of Material Removed from each class of Trough.

Date	Total amount of material removed (lb.)			Average amount of material removed from each trough (lb.)	
	Calcium carbonate		Calcium carbonate dicalcium phosphate	Calcium carbonate only	Calcium carbonate + dicalcium phosphate
	Trough 1	Trough 2			
April 1951—November 1951	373	308	449	42·6	56·1
November 1951—March 1952	55	4	100	3.7	12·5
TOTAL CONSUMPTION April 1951—March 1952	428	312	549	46·3	68·6

TABLE II. Showing the Amounts of Phosphorus, expressed as P_2O_5, Removed from the Troughs, and the Amounts Removed per Cattle Beast

Date	Total amount removed (lb.)	Average amount removed from each trough (lb.)	Average amount eaten per cattle beast per day (oz.)
April 1951—November 1951	117·1	14·6	0·1
November 1951—March 1952	26·1	3·3	0·04
TOTAL CONSUMPTION April 1951—March 1952	143·2	17·9	0·08

be about one-eighth of that of a dry cow (Groenewald, 1950), have not been considered in calculating the above figures. This therefore strengthens the conclusion that the animals on the grazing failed to select to advantage. Further confirmation comes from the fact that the owners of this stock have been unable to see any improvement in their animals. The aphosphorosis was not corrected.

Discussion

Phosphorus-deficient cattle certainly show a generally depraved appetite but the specific selection of materials of high phosphorus content, e.g. bones, is in all probability due to one of the following reasons : (1) purely a matter of chance; (2) learnt response resulting from an experience of well-being following the selection of bones; or (3) imitation of the behaviour of other animals which have learned to select.

The argument against the proposition that phosphorus-rich material is "instinctively recognised" by phosphorus-deficient cattle is further strengthened by two other considerations. Firstly, cattle which chew bones do not show a predilection for all phosphorus-rich materials. Theiler & Green (1932) have admitted that no obvious preference is shown for such materials as mineral phosphate, precipitated calcium phosphate, and sodium phosphate. Secondly, the depraved appetite does not invariably disappear when the aphosphorosis has been corrected (Green, 1925), and certainly osteophagia cannot be relied upon as a sure sign of phosphorus deficiency. It therefore appears that, rather than any specific desire for material rich in phosphorus on the part of deficient cattle, there is a generally depraved appetite which in its milder form is limited to the consumption of relatively palatable, although normally uneaten, material, *e.g.* dry bones and "pendant washing on the village green", and in its more severe forms results in the eating of such abnormal items as decomposing flesh and live tortoises.

Summary

1. Ninety cattle, representative samples from which showed low blood-phosphorus levels, and 500 sheep grazing 5,500 acres of rough pasture in the Isle of Skye, where both the soil and pasture were low in phosphorus, showed evidence of osteophagia and allotriophagia.
2. These animals, when offered a choice between a calcium supplement and a calcium-phosphorus supplement, failed to show a significant preference for the latter. Although they had the opportunity of doing so, they failed to remedy their deficiency by eating sufficient quantities of a phosphorus supplement.

Acknowledgments

We wish to acknowledge our indebtedness to Messrs. D. MacAskill, H. MacRae, A. MacLennan and W. MacPherson, on whose land and with whose animals these observations were carried out. We are grateful also to Mr. A. W. Boyne for statistical advice and to Mr. J. L. Corbett for general assistance.

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Some Notes on the Behaviour of Hill Sheep*

By R. F. HUNTER

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In the course of a study on the preference of hill sheep for typical hill sward types, the opportunity was taken to make some observations on the behaviour of the sheep. As the study was not principally of behaviour the methods used were unsuitable for a critical study.

The site of the observations was Overshiels Farm, Midlothian, Scotland, and the pasture lay between 950 and 1,250 feet above sea level. The stock were Scottish Blackface breeding ewes which are maintained on the pasture throughout the year, as is the practice in hill farming. It should be noted that the preferences of sheep for different sward types are very marked, as has already been shown by Boulet (1939), and that the degree of preference varies seasonally.

Hill sheep, when bought with the farm to which they belong, are counted as having an acclimatisation value and a higher price is obtained for them than they would bring in the open market. This value is probably based on an acquired immunity to diseases prevalent on the farm, and on the sheep's knowledge of the pasture.

General Observations

When rain was heavy and driving, the sheep stopped grazing and faced away from it. After a night of rain, followed by a damp humid morning, they were late in beginning to graze. In such conditions they did not begin to graze until a short time after sunrise; normally they begin to graze before it.

The ewes appeared to be sensitive to exposure (the cooling power of the air) but this sensitivity was more acute at certain times of the year. During winter they continued to graze under all conditions except those approaching a blizzard. In spring, and during lambing time, they were much more sensitive to exposure and sought shelter under conditions to which they would not have reacted a month or so before. Indeed, it was only during lambing time, and for a month or so afterwards, that behaviour appeared to be affected to any degree by exposure.

The sheep appeared to have an intimate knowledge of their pasture. At the time of year when they were grazing the young heather they were often observed at first light on a part of the pasture from which they could not see the young heather areas; nevertheless, they moved in a straight line towards the young heather. This suggests not only a knowledge of what they wanted to graze but also of its exact location on the pasture. In winter they were frequently seen at first light lying in the lower parts of the pasture. This area was covered with hoar frost, as was the whole hill. The moment the sun rose the sheep moved towards those parts of the pasture from which the sun would first lift the frost.

The pasture, being part of a hill, was sited half on the low-lying ground and half on the high ground. In general the low ground was the grazing area and the high ground the night resting area. This different use of the two parts of the pasture may have been instinctive, but was more probably the result of training, as it is the practice in hill farming to turn the sheep up to the high ground in the evening. The sheep will themselves, at most times of the year, come down to the low ground in the morning to graze the better quality herbage which is found there. In winter they tend to stay on the low ground, especially in rough weather and after the New Year. There is, however, one aspect of their behaviour in this respect which is not readily explained.

From October to about the end of January the shepherd at Overshiels did not herd the sheep except for special reasons, e.g., tupping and times of storm, believing that the sheep best know where to find their own grazing. This is quite a prevalent belief among Border shepherds and they disturb their sheep as little as possible during this period. The sheep, nevertheless, did not graze at random but showed a marked preference for the high ground, to which they moved without being herded. On some days at this time of year, they were seen at first light on the low ground where they would stay throughout the day, while on other days, around 11 a.m., they would move as a flock,

*Part of a thesis submitted for the degree of Ph.D. of Edinburgh University.

to the high ground, where they remained until dark.

They had not been disturbed by a shepherd whistling, or a dog barking, and it may be that this behaviour was a reaction to weather conditions. Similar behaviour was found in the Red Deer (Darling 1937), and a modified form may persist in the domesticated sheep.

Without a critical study it is impossible to decide which features of hill sheep behaviour result from herding and which are innate. Furthermore, behaviour which has been learnt by herding may have been taught some years previously and will persist in a flock composed of sheep in regular ages, as the young sheep will learn in turn from the older.

Resting and Grazing

In the course of this study the total number of sheep in a 76 acres area which was being observed, and the number of those which were lying down, was noted. This area was part of that grazed by a heft of 80 sheep. (A heft is a Scottish term used to denote a number of sheep whose grazing range is restricted to a particular part of the hill pasture. A hill flock is generally composed of a number of hefts. The hefts are not fenced in but are kept on their ground by shepherding.) On some days no sheep were in the observed area, on others all 80 sheep grazed the area, and invariably the number fluctuated throughout the day. Observations were made at hourly intervals from dawn to dusk on 76 days during the 25 month period, September, 1950, to September, 1952.

The number of resting sheep was calculated as a percentage of the total number of sheep observed at each hourly interval (see Table I and Fig 1).

The periods of rest were related to times of sunrise and sunset during the long days from April to September. The sheep began to move from the high ground before sunrise and, after a period of grazing in the course of moving to and after arriving at the low ground, they rested for one or two hours then began to graze again. There was another period of rest in the afternoon, less general in the sense that the sheep did not all rest at approximately the same time. In the late afternoon they began to move up the hill and started to settle down shortly before sunset.

No evident periodicity in resting emerges from these figures, but it is unlikely that this would be clearly noted unless observations were made of the behaviour of individual sheep.

During the short days, from October to March, the sheep rested much less than in the long days of summer, and only one period, and that a very clearly marked period, of rest occurred. This took place before mid-day, and

TABLE I. Average Percentage of Sheep Resting during Daylight Hours (Period Sept., 1950—Sept., 1952).

G.M.T. (hrs.)	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Jan.								0	0	25	0	0	0	0					
Feb.						0	2	30	68	67	0	0	0	0	58				
Mar.					9	9	8	14	37	7	15	8	5	15	37				
Apr.				36	25	13	8	26	5	0	13	20	7	8	4	36	55		
May		5	64	41	31	6	5	21	10	10	15	10	26	17	1	0	36	54	
June	10	66	42	41	48	21	13	52	14	40	12	36	40	37	34	2	21	65	88
July	2	9	52	43	40	20	60	15	29	12	3	14	14	25	22	7	11	22	
Aug.		10	20	54	51	30	30	22	18	27	25	30	16	21	16	15	35	50	
Sept.				0	24	25	27	41	36	48	21	14	18	5	9	3	50		
Oct.				0	0	8	45	38	45	16	12	7	1	2	0	45			
Nov.					0	1	15	52	54	14	4	2	0	0	0				
Dec.					0	0	89	33	44	30	16	0	0						

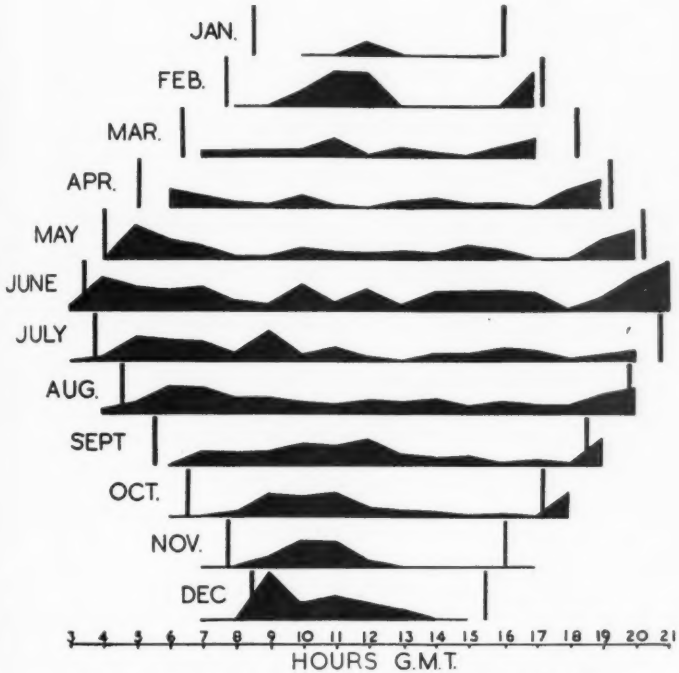

Fig. 1. Percentage of Sheep Resting during Hours of Daylight. (Thick upright lines are drawn at hour of sunrise and sunset to a vertical scale of 100%).

according to the day-length, at some time between 0900 hours and 1200 hours G.M.T.

If a comparison is made between those months in the first (March-May) and second (August-October) parts of the year which have similar day-lengths, it will be seen that rest during the day was much shorter during the first part of the year. This behaviour was perhaps related to the differences in available grazing and environmental temperature, and to the greater nutritional requirements of the milking ewe in spring.

No observations were made at night, but Crofton (1949) remarks that hill sheep graze and move very little during the hours of darkness. Of the hill sheep observed by him only 10 per cent. were grazing at night while 90 per cent. were grazing during the day. Wallace (1884) noted that hill sheep do not eat during the short summer nights but do so in the long winter nights between the hours of 11 p.m. and 2 a.m.

The spring of 1951 was much more severe than that of 1952 and grazing was more scarce in the former year. It is interesting to note that during 1951 the average number of sheep resting in the daylight hours of April was 4 per cent, and of May 8 per cent., while the corresponding figures for 1952 were 17 per cent. and 18 per cent.

Hill sheep are more active than lowland sheep during the hours of daylight. Unfortunately, we have no data for the night behaviour of hill sheep, but we believe it to be quite probable that they are more active than lowland sheep over the 24-hour period.

Table II shows the comparison between the average times spent resting during the hours 07.00—19.00, in the months April-September by lowland sheep, for which the figures have been adapted from Tribe (1949) and the hill sheep at Overshiels.

Hill sheep are more active than sheep under the conditions of Tribe's observations.

Studies of hill sheep behaviour would be of practical advantage as some problems of hill sheep farming can only be solved by a study of the behaviour of the sheep under natural

TABLE II. Percentage time spent resting in the hours 07.00—19.00 by Lowland and Hill Sheep.

	Apr.	May	June	July	Aug.	Sept.
Lowland (Tribe 1949)	32	32	40	45	45	47
Hill (Overshiels)	13	13	29	21	26	23

conditions. For example the siting of shelter belts should be based on a clear understanding of the sheep's need and use of shelter under natural conditions.

Acknowledgments

The writer wishes to thank Professor S. J. Watson and Mr. R. G. Heddle, both of the Edinburgh and East of Scotland College of Agriculture, for their advice and encouragement, and Lord Whitburgh for permission to pursue this study of Overshiels.

Summary

Observations were made on the behaviour of Scottish Blackface sheep on a hill pasture in south-east Scotland.

(1) Hill sheep have a knowledge of their pasture and this knowledge is a component of the acclimatisation value of a hill flock.

(2) They are sensitive to exposure, but only in spring is this an important factor in determining the location of grazing.

(3) On the pasture as a whole the location of grazing varies seasonally. The reason for this is obscure, but may arise from either instinctive or learnt behaviour and be related to available grazing, meteorological conditions, nutritional requirements and the presence or absence of lambs.

(4) Periods of rest are related to times of sunrise and sunset. Rest is greater in the long days of summer than in the short days of winter. It is less in the spring months from March to May than in the autumn months from August to September, both periods having similar day lengths.

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Book Reviews

Animal Courtship. By MAURICE BURTON. London: Hutchinson. 1953. Pp. 267. 16s.

This well-written work provides a neat and factual account of various aspects of courtship through a wide range of animal species. As such it will undoubtedly help materially the general appreciation of animal behaviour studies by the lay public. The excellent illustrations by Jane Burton add materially to the value and readability of the work. It is appreciated that this book has been written for a wide public, but it does seem nevertheless that when the author has gone to such trouble to piece together material from an extremely wide variety of sources, the book should lack adequate documentation. Even footnote references would have rendered *Animal Courtship* of considerably greater value to the serious student.

Bird Ringing. By R. M. LOCKLEY & ROSEMARY RUSSELL. London: Crosby Lockwood. 1953. Pp. viii + 119. 9s. 6d.

In five chapters and three appendixes this little work provides a succinct account of almost all aspects of Bird-ringing. In style it departs materially from the normally somewhat discursive approach of the senior author, but its readability is by no means impaired in consequence, and it is altogether a commendable monograph that will be read and used by all ornithologists, and will constitute a standard work of reference on this important technique.

Animals and Men. By BERNARD KATZ. Translated by Hannah Steinberg & Arthur Summerfield. London: Penguin Books. 1953. Pp. 192. 2s.

The proprietors of the Pelican series are to be congratulated on their publication of the revised translation of Bernard Katz's work, which replaces the 1935 translation hitherto in use in English-speaking countries. The general outline of the work remains unchanged, but there have been a number of additions and amendments. The scope of the text does not embrace much of the modern research on ethology, but this nevertheless remains one of the most useful of the more general elementary texts on animal behaviour, and ought to be in the possession of every serious student, as well as being a most helpful work to members of the general public. The editor of the series suggests in his preface that *Animals and Men* ought to be read by every intelligent farmer and animal owner, as well as by all those who, while not keeping animals themselves, are confronted by the economic problems arising from the depredations of the brown rat and other pests.

Katz's review of certain aspects of avian behaviour has probably never been bettered.

Mammalian Hybrids: A Check-List with Bibliography. Technical Communication No. 10 of the Commonwealth Bureau of Animal Breeding and Genetics, Edinburgh. By ANNIE P. GRAY. Farnham Royal: Commonwealth Agricultural Bureaux. 1954. Pp. x + 144. 21s.

As Dr. W. G. Osman Hill remarks in his Foreword, zoologists generally and mammalogists and geneticists in particular will welcome the present annotated compilation, both as a work of reference and as a reliable guide to the large number of mammalian hybrids reported in the literature. The study of inter-specific hybridisation is, of course, of considerable interest to behaviourists, and among other groups of vertebrates we have, for example, the recent ethological data of Poulsen.

The present Check-list has clearly been prepared with meticulous care, and the probable accuracy of each record is stated. As the author observes, there are obvious objections to the practice that has had to be adopted of giving specific rank to those domestic animals that are of diverse origin, but this is the only convenient way of fitting such animals into the alphabetical arrangement that has been employed.

In view of the recent writings of Lorenz on the behaviour of domestic dogs of different origin, it is interesting to observe that there appears to be no record of a hybrid between *Canis lupus* and *C. aureus*, or the reciprocal.

ERRATUM

The British Journal of Animal Behaviour, Vol. II, No. 1, p. 38.

Delete "INFRA-RED" from the title of the paper by J. B. S. Haldane & H. Spurway.

BIRD STUDY

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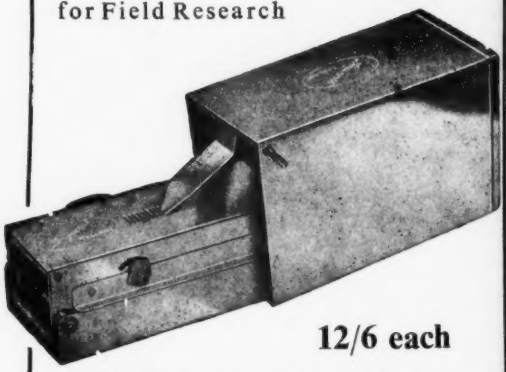

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